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A NEW MENDELIAN RATIO AND SEVERAL TYPES OF LATENCY

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Introduction

In two papers presented before the Botanical Society of America at its annual meetings in New Orleans (1905) and New York (1906), I discussed the question of latency as exemplified by certain color-characters in common garden beans (*Phaseolus vulgaris*). These papers were published in reversed order in Science, May 7 and 24, 1907.

It was shown that certain characters appeared in the hybrids, of which no indication was found in either parent, and the origin of these novelties was traced to unseen Mendelian units possessed by the white bean (White Flageolet) used in the various crosses. The new characteristics were a mottled color-pattern, *M*, and a blackener or enzyme, *B*, which acts upon brown or yellow pigments, *P*, to produce anthocyan, the presence of the latter resulting in black or various shades of violet to reddish purple seed-coats. It was assumed that the brown and yellow beans used in these crosses have the gametic formula, *Pbm*, the black bean the formula, *PBm*, and the white the gametic formula, *pBM*. In crossing the white bean with any of the self-colored beans the three dominant units were brought together, resulting

in a purple mottled F_1 (*PBM*). It was the occurrence of this purple mottled F_1, no matter which pigmented bean was used, that led to my conclusions regarding the latency of a mottled color-pattern and a melanizer in the white bean, and also to the prediction that F_2 would consist of the five forms—purple mottled, black, brown mottled, brown (more properly, dark orange), and white, —in the well-known tri-polyhybrid ratio, 27:9:9:3:16.

An Unexpected Ratio and its Significance

At the time my last report was made, the count of the F_2 hybrids had not been completed, but the five predicted types were clearly presented. On summing up the results of the census of the numerous F_2 hybrid families, it was found that the ratio was not as predicted, but the mottled and self-colored beans occurred in all cases in approximately equal numbers, resulting in the ratio 18:18:6:6:16, or, reduced to its lowest terms, 9:9:3:3:8. To be exact, in the cross between Ne Plus Ultra (dark orange yellow, called "brown" in my notes) and White Flageolet, 10 families gave 133 purple mottled, 114 black, 40 brown mottled, 50 brown, 105 white, and 6 doubtful. Similarly, in the cross between Long Yellow Six Weeks (light yellow) and White Flageolet, 13 families gave 154 purple mottled, 159 black, 39 yellow mottled, 59 yellow (or brown), 160 white, and 12 unclassified. In the cross between Prolific Black Wax and White Flageolet, 3 families gave 53 purple mottled, 59 black, 44 white and 4 unclassified.

On comparing these results with those published by Tschermak[1] it is found that they are in perfect accordance with them, as he also found in a number of similar crosses, an equality between the mottled and self-colored beans. But our conclusions were diverse as to the source of the mottled pattern, I assuming that the mottled factor was brought into the combination by the white

[1] Tschermak, E. Weitere Kreuzungsstudien an Erbsen, Levkojen und Bohnen. *Zeitschr. Landw. Versuchsw.*, 7, pp. 533–638, 1904.

bean as a simple Mendelian unit, while he assumed that a mottled factor was carried as a "cryptomere" by the pigmented bean and that the white bean acts simply as a releasing agent or activator which allows or compels the latent mottling to become apparent.

The ratio 18:18:6:6:16 must have at first a very unfamiliar look to the student of genetics. It was not explained by Tschermak, but was separated by him into two groups of 9:3:4, wherein the interrelations of the several terms need no explanation.

The census of my second generation was completed shortly after the appearance of De Vries's[2] interesting account of "Twin hybrids" in Œnothera, and the suggestion lay at hand that this ratio presented by Phaseolus might be a case of twin di-hybrids, the first and second terms of the ratio, as also the third and fourth terms, being in each case different phases or aspects of a single unit, which might be expressed thus 9A:9∀:3B:3ᗺ:8W. While such an hypothesis would fit the conditions presented by the F_2, it was seen very soon that it does not harmonize with the occurrence of a uniformly purple mottled F_1, nor with the splitting phenomena of F_3, a portion of which has been already examined. A consideration of the F_1 and F_3 shows that there are three distinct units involved, as was stated in my earlier papers, namely—a pigment factor, *P*, a blackener, *B*, and a mottled pattern, *M*.

If all of these characters behaved according to the simple Mendelian method, the ratio would be that previously predicted, and out of every 64 individuals, on an average, 27 would have purple mottled seeds, and 9 black. In order that the number of individuals having purple mottled seeds shall be equal to the number having black seeds, it is necessary that of the 27 that should on theoretical grounds be purple mottled, 9 must show no purple mottling but must be black, though it contains the dominant mottle factor, *M*. This group of 27 purple mottled

[2] De Vries, H. On Twin Hybrids. *Bot. Gaz.*, 44, pp. 401–407, D 1907.

individuals belonging to the theoretical F_2 ratio consists of the following eight types:

1 *PBMPBM*
2 *PBMPBm*
2 *PBMPbM*
2 *PBMpBM*
4 *PBMPbm*
4 *PBMpBm*
4 *PBMpbM*
8 *PBMpbm*
27

There is only one basis on which a group of 9 individuals having a common gametic feature may be derived from this group, namely, on the ground of homozygosis with respect to any single allelomorph. Thus, there are 9 homozygotes with respect to *P* (1 *PBMPBM* + 2 *PBMPBm* + 2 *PBMPbM* + 4 *PBMPbm*), 9 homozygotes with respect to *B* (1 *PBMPBM* + 2 *PBMPBm* + 2 *PBMpBM* + 4 *PBMpBm*), and 9 homozygotes with respect to *M* (1 *PBMPBM* + 2 *PBMPbM* + 2 *PBMpBM* + 4 *PBMpbM*), and the assumption that any one of these groups will give self-colored beans will answer the requirements of the empirical F_2 ratio, 18:18:6:6:16.

The only way in which it is possible to decide which of these three possible groups of 9 homozygotes is responsible for the equality of the mottled and self-colored types is to test their applicability to the other generations, since they all fit equally well the ratio found in the second generation. If homozygotes with respect to *P* hide the presence of *M*, it will be impossible to find an individual with mottled seeds which will not give a progeny, one fourth of which will be white-seeded; but of the F_3 families already examined, a number have been found which, while continuing to give mottled and self-colored beans in the ratio 1:1, have failed to produce any whites. If the homozygotes with respect to *B* are responsible for the latency of *M*, some brown or brown

mottled offspring would be produced by every purple-mottled parent, and there would be no equality between the purple-mottled and black in many families of the third and subsequent generations; but those F_3 families which have been thus far investigated show a number of instances in which purple mottled parents produce no brown or brown mottled young and there is a continued equality between the mottled and self-colored offspring of such parents. The remaining possibility, namely, that individuals which carry the mottled pattern, *M*, but are homozygous with respect to that character, are not mottled but self-colored, is the only one that fits all of the observed facts. The mottled color-pattern must be heterozygous in order to become apparent in the hybrids.

We may then indicate the composition of the group of individuals of F_2 which carry the dominant mottling factor, *M*, and the expectation as to the composition of the offspring which each will produce in F_3 as follows:

1 *PBMPBM* = Bl(Bl) (*M* latent in all).
2 *PBMPBm* = PM(1PM:1Bl) (*M* latent in ½ the Bl).
2 *PBMPbM* = Bl(3Bl:1Br) (*M* latent in all).
2 *PBMpBM* = Bl(3Bl:1W) (*M* latent in all).
4 *PBMPbm* = PM(3PM:3Bl:1BrM:1Br) (*M* latent in ½ the self-colored).
4 *PBMpBm* = PM(3PM:3Bl:2W) (*M* latent in ½ the Bl and ¾ the W).
4 *PBMpbM* = Bl(9Bl:3Br:4W) (*M* latent in all).
8 *PBMpbm* = PM(9PM:9Bl:3BrM:3Br:8W) (*M* latent in ½ the self-colored and ¾ the W).

It will be seen from this scheme that the mottled color-pattern could exist and does exist as a latent (*i. e.*, invisible) character in pigmented beans just as well as in the white bean, which is contrary to the assumption made, when I insisted that the mottled pattern must have come from the white bean. It is also obvious that the mottled

pattern could not exist in both the pigmented and white beans used in these crosses, as in that case the F_1 hybrids would have been homozygous with respect to this character and would have been black self-colored instead of purple mottled. In attempting to settle the question as to the origin of this mottled color-pattern I have carefully examined the results recorded by Tschermak and find evidence that at least one pure-bred pigmented bean must possess the mottled pattern while another does not. Whether the white beans used by him carried latent *M* can not be settled at present, but it is now plain that he may have been right in referring the mottling factor to the pigmented beans. My White Flageolet as well as all the white beans used by Tschermak may not have the mottled pattern, and the gametic formula of the White Flageolet should then be written *pBm*, instead of *pBM*.

This question can only be settled by further careful crossing. The evidence derived from Tschermak is as follows: In the cross between "Hundert für eine" (light yellowish brown) and "Mettes Schlachtschwert" (white) there was no mottling in the offspring; "Hundert für eine" crossed with "Schwarze Neger" (black), both self-colored, gave mottled offspring. Now according to my hypothesis, if "Schwarze Neger" carries the mottled pattern, "Hundert für eine" does not have it, and in turn, "Mettes Schlachtschwert" must not have it. If "Schwarze Neger," on the other hand, does not carry the mottled pattern, "Hundert für eine" has it, and in this case "Mettes Schlachtschwert" must also carry it. We can not say certainly, therefore, that the white "Mettes Schlachtschwert" does or does not have the mottled pattern, but on theoretical grounds either condition would be equally possible.

Among the corollaries of the explanation here given for the ratio 18:18:6:6:16 is not only the fact already given that the mottled pattern may be carried by the pigmented bean invisibly quite as well as by the white bean, but also, since the mottled beans are heterozygous with re-

spect to *M*, it would be impossible to have any of them breed true, *i. e.*, the mottled bean is in the same category in this respect as the famous Blue Andalusian fowl. This conclusion is supported by 48 families of the third and fourth generations reported by Tschermak and by over sixty families of the F_3 from my own mottled hybrids which have been already examined. Not one instance has been found in which the offspring of a mottled hybrid were even approximately all mottled.

The existence of pure-bred mottled races raises the interesting question as to what relation exists between these mottled hybrids which are heterozygous and can not breed true and the true-breeding mottled varieties. Tschermak[3] shows that in crosses between constant mottled races and self-colored races, the mottled pattern acts as a typical Mendelian dominant, the hybrids splitting in F_2 and subsequent generations in the ratio, 3 mottled:1 self-colored.

Latency due to Separation

With respect to the question of latency since the purple mottling may not be a latent character of the White Flageolet, the type of latency discussed in my previous papers was only certainly exemplified by the pigment-changer, *B*, carried by the white bean. This type of latency is discovered by the production of a novelty when two allelomorphs are brought together, one or each of which, when acting alone, produces no visible character. Thus the black or purple color of these hybrids is due to the combination of the yellow or brown pigment of the pigmented parent and the colorless pigment-changer borne by the white parent. It may be called *latency due to separation* since patency is brought about by recombination. In my first paper on latency,[4] issue

[3] *Loc. cit.*

[4] Shull, G. H. Some Latent Characters of a White Bean. *Science*, N. S., 25, pp. 828–832, May 24, 1907.

was taken with Lock[5] regarding his assumption that novelties which appeared in crosses between certain peas were due to inactive units which became active on crossing. Lock[6] has since reconsidered that case and independently come to the same conclusion that I reached, namely, that the spotted seed-coat was introduced by the white-coated pea in which it was invisible owing to its separation from the pigment-producing factor. This is not an uncommon type of latency and seems to be the only type included by writers who have treated the subject of latency from the Mendelian view-point. It gives rise to such modifications of the Mendelian ratios as 9:3:4, 9:7, 27:9:9:3:16, 27:9:28, etc., instead of the theoretical 9:3:3:1 and 27:9:9:9:3:3:3:1. Some of these modified ratios are of more common occurrence, and are more familiar, than the unmodified ones, perhaps owing to the fact that albinism has been so frequently involved in the Mendelian investigations. Characteristics which are rendered latent by separation in the course of Mendelian hybridization have been called "masked" characters by Punnett.[7] This is not a particularly apt term for latent characters of this type, and would be much more appropriately applied to cases of latency due to hypostasis discussed below.

Latency due to Combination

The existence of mottling as a latent characteristic in pigmented beans, due to the fact that it only becomes apparent when in the heterozygous condition, is obviously of an entirely different type. Instead of being a phenomenon of separation, it is due to the union in the same zygote, of two dominant allelomorphs, either of which alone will produce a manifest character, but

[5] Lock, R. H. Studies in Plant Breeding in the Tropics. *Ann. Roy. Bot. Gard. Peradeniya*, 2, pp. 299–356, 1904. See p. 241.

[6] Lock, R. H. On the Inheritance of Certain Invisible Characters in Peas. *Proc. Roy. Soc.*, B, 79, pp. 28–34, 1907.

[7] Punnett, R. C. Mendelism. 2d ed., pp. viii + 85, 1907, London: Macmillan & Co. See pp. 47–53.

which, when acting together, produce none. This may therefore be called *latency due to combination,* since patency is brought about by separating the two allelomorphs whose union effaces their characteristic manifestation. If the White Flageolet carries the mottling factor, *M,* as was at first supposed, the appearance of mottling as a novelty in the first generation hybrids was due not alone to that fact, but just as much to the fact that the pigmented bean does not carry the mottled factor; or if, on the other hand, it should prove true on further investigation that the white bean does not carry the mottled factor, the mottled F_1 is due to this very fact, quite as much as to the fact that the colored bean does possess it.

The conclusion, reached in my previous papers, that the primitive bean was probably purple mottled and that the purple mottled condition is therefore an atavistic one, seems to be left in some doubt, because of the existence of two types of mottling, one of which behaves as a typical Mendelian unit as shown by Tschermak, the other having the peculiar faculty of losing its external manifestation the instant it becomes homozygous. I have no doubt that in some form the mottling unit is a primitive one, but whether the ancestral bean possessing that unit was mottled or self-colored would depend entirely on which type of the mottling unit it carried. In order to breed true it is necessary that both eggs and sperms shall all carry the mottled factor, and if this mottled factor were of the latter type, the beans produced by the union of such sperms and eggs, being homozygous with respect to mottle, would be self-colored, while if the mottle was of the former type, the homozygous beans would be mottled. The conclusion as to the allelomorphic composition of the original bean is probably correct, but as to its external appearance, it may as well have been black as mottled.

The peculiar behavior of the purple mottled allelomorph in my hybrids and in most of Tschermak's, may have a

very important bearing upon the interpretation of what are known as mid-races, *i. e.*, races which regularly produce two forms in about equal proportions, for, as has been seen, the mottled beans of all the hybrid families which did not have a mottled bean as one of its original pure-bred ancestors, constitutes a mid-race. This fact was recognized by Tschermak (*loc. cit.*, p. 47), though he attributed it to an unexplained effect of cross-fertilization, and not to the characteristic behavior of a definite Mendelian allelomorph. Other mid-races may likewise represent instances of latency due to combination. Wherever there is a double series of characters occurring in about equal numbers in the progeny of a self-fertilized individual, this type of latency should be looked for.

Purple punctation and brown flecking, which occur as novelties in the seed-coats of hybrid peas, were found by Tschermak to behave in a manner quite analogous to the mottling in beans, the first generation showing dominance of the novelty and subsequent generations always splitting into the punctate and non-punctate or the flecked and unflecked, respectively, and these no doubt are also cases of latency due to combination. Lock[8] has shown, on the other hand, that when certain mottled and spotted peas are crossed with self-colored peas, the mottling and spotting act as typical Mendelian dominants capable of extraction as characteristics of pure-breeding races, which ought to be expected, since the homozygous parental strains possessed these characters. The apparent discrepancy between his results and those of Tschermak will be fully explained if we assume that there are two types of these color-pattern characters in peas, as there are in beans.

In all of these cases of latency due to combination, the two units involved are of the same kind, so that the latency occurs only in the homozygous individuals, thus resulting in a striking contrast between homozygotes and

[8] Lock, R. H. On the Inheritance of Certain Invisible Characters in Peas. *Proc. Roy. Soc.*, B, 79, pp. 28–34, 1907.

heterozygotes. There are many other cases in which the homozygote and heterozygote show marked and often unexpected differences, the case of the Blue Andalusian fowl being one of the best known of these, but the heterozygous type of the Blue Andalusian fowl or other similar forms is not a case of latency at all, since no hidden allelomorph is brought to light as a result of heterozygosis, but only an unexpected external manifestation.

Latency due to Hypostasis

A third type of latency has also appeared in these bean hybrids, as best exemplified by a cross between the Prolific Black Wax and the Ne Plus Ultra, and between Prolific Black Wax and Long Yellow Six Weeks. In both of these crosses, besides the black and orange or black and yellow which were expected in the ratio 3:1, there have appeared a considerable number of beans of a dark seal brown or a dark greenish brown color. It is certain that these dark brown beans owe their color to the latency of a dark brown factor in the black bean. It has not been an infrequent occurrence to find black beans, not quite perfectly matured or which have been more or less weathered, that show this brown color apparently underlying the black. In this case the appearance of the novelty is due to the presence of a characteristic which can not be seen (*i. e.*, which is latent), for the simple reason that the black pigment possessed by the same bean is so intense as to cover over and hide the brown pigment. The independence of the brown and black pigments allows them to be separated into different individuals upon crossing the black with some other color.

Letting *D* represent this dark brown factor, the gametic formula for the black bean is *BD*, and for the orange brown and yellow beans, *bd*. This assumption leads to another rather unfamiliar modification of the Mendelian ratio, since the F_2 should consist of black, brown and orange or yellow in the ratio 12:3:1. The actual ratios are in essential accord with this expectation though there

are rather wide discrepancies due to the fact that the categories were not as carefully distinguished at first as they should have been. Thus in the case of the cross of Prolific Black Wax (black) with Ne Plus Ultra (dark orange or "brown") many of the dark brown beans were recorded at first simply as "brown," and the ratio found, 174 black:47 seal-brown:26 "brown," shows clear evidence of the extent of error thus produced. A deficiency of black is also apparent and is no doubt due to the recording of some weathered blacks, as dark brown. In the cross between Prolific Black Wax and Long Yellow Six Weeks, the deficiency in the blacks and corresponding excess in the dark brown is even more striking, giving the ratio, 155 black:55 dark brown:9 yellow:5 unclassified, theory requiring 168 black:42 dark brown:14 yellow. This factor *D* is also found to be present in the White Flageolet, where, like the black factor, *B*, it is latent by separation.

The occurrence of dark brown as an invisible character in the black bean may be called a case of *latency due to hypostasis,* following the terminology suggested by Bateson.[9] The unexpected character is not inactive, but its characteristic manifestation is invisible because it is hidden or inhibited by some other quality, and can only become visible when the overlying or inhibiting quality is removed by some means.

This type of latency is no doubt very common, as it is involved in many cases of simple dominance, as that term is generally understood. If the "presence and absence" hypothesis has general validity (and there is a very great preponderance of evidence in favor of it), the term "dominance" should be limited to the relation of the presence of any characteristic to the absence of that same characteristic, and should not be used for the relation between two different positive allelomorphs by virtue of which one hides the presence of the other. Bateson

[9] Bateson, W. Facts Limiting the Theory of Heredity. *Science,* N. S. 26, pp. 649–660, November 15, 1907.

applies the terms "epistatic" and "hypostatic" to the relative capacity of one unit to hide or to be hidden by another, owing to what I call latency due to hypostasis. As a simple illustration, a cross between a pea with yellow cotyledons, Y, and one having green cotyledons, G, shows Y dominant over its absence, y, and not over G. This would become immediately obvious if we could cross the yellow pea with still another type, say with one having colorless cotyledons. The correct gametic formula for the yellow pea is not Y but YG, in which the green is latent owing to the fact that Y is epistatic to G. The gametic formula of the green pea is yG.

That this is a correct interpretation of the apparent dominancy of one positive allelomorph over another is shown by some of my bean crosses. Thus Ne Plus Ultra (dark orange yellow) crossed with Long Yellow Six Weeks (light yellow) produced in 14 F_2 families, 382 orange yellow : 130 light yellow, an apparent dominance of orange over light yellow. That the light yellow is latent in Ne Plus Ultra and is not the recessive condition of the orange yellow allelomorph is proved by the fact that in the F_2 families of the cross between White Flageolet and Ne Plus Ultra, light yellow beans appear. Letting O represent the orange allelomorph and Y the yellow one, the gametic formula of Ne Plus Ultra with respect to these two factors is OY, that of the yellow bean is oY, and that of the white bean likewise oY.

The ratio, 12 : 3 : 1, presented by the crosses of Prolific Black Wax with Ne Plus Ultra and Long Yellow Six Weeks, has been reported for but one other case so far as I know, though it ought not to prove very uncommon. It will appear in the F_2 of any cross which produces an F_1 of the form $ABCab$ with B hypostatic to A, C hypostatic to both A and B, and neither A, B, nor C latent from any other cause. In these beans the crosses are of the type $ABC \times abC = ABCab$, *i. e.*, both B and C are latent in the one parent and no latent characters are demonstrated in the other. The same ratio will result from a

cross of the type $AbC \times aBC = ABCab$ provided the same relations exist among the several allelomorphs as before. In this case the character C is latent by hypostasis in both parents. This condition has been realized by Toyama[10] in hybrids between the common Japanese white silk-worm and the Siamese striped silk-worm in both of which a "pale," unmarked type is latent by hypostasis. The F_1 is uniformly striped like the Siamese, and the F_2 consists of striped, "white," and "pale" in the ratio 12:3:1. Toyama's statement that the "pale" character was in the "dormant" state indicates a misconception of the nature of latency due to hypostasis.

Latency due to Fluctuation

Another very potent cause of latency is to be found in fluctuation. It is well known that many of the less marked qualities of plants do not appear under unfavorable conditions of growth. By growing the offspring of these poorly developed individuals under favorable conditions they may be shown to possess all the characters of other members of the race to which they belong. Invisibility produced by this cause may be called *latency due to fluctuation.* Patency is brought about by good feeding, room for full individual expression, etc. As a specific example, I may mention my experience with several biotypes of *Bursa bursa-pastoris* (L.) Britton. These differ from one another by certain characteristic lobings of the leaves, and these characters have proved, on crossing, to be typical Mendelian unit-characters. However, by growing the plants belonging to any of the several biotypes under sufficiently unfavorable conditions they may be made to produce seeds while bearing only the unlobed juvenile type of leaf. The Mendelian rosette characters are then wholly invisible or latent. If the

[10] Toyama, K. Studies on the Hybridology of Insects. I. On some silkworm crosses with special reference to Mendel's Law of Heredity. *Bull. Coll. Agr. Tokyo Imp. Univ.*, 7, pp. 259–393, pls. VI–XI, July, 1906. See pp. 348–353 and pl. X, III, *a*, *b*, and *c*.

offspring of such plants are grown under favorable conditions the latent characters are again rendered patent, showing that the loss of external manifestation has had no influence upon the allelomorphs themselves; they were present in the badly developed specimens, but were invisible because a sufficiently late stage of differentiation was not attained to permit them to express themselves.

Another striking case in which the latency of a Mendelian character, perhaps due to fluctuation, has been fully demonstrated, is in the cross between blue and white Indian corn investigated by Lock.[11] The blue is, in general, dominant over the white, but the white grains are always in excess of expectation, sometimes more, sometimes less; subsequent breeding tests with the whites show that a sufficient proportion of them are heterozygous, instead of extracted recessives, to make up the deficiency found in the number of blues in the preceding generation. It is not impossible, as Lock suggests, that further investigation of this case will discover some other cause than fluctuation for the latency of the blue aleurone layer in these white-grained heterozygotes.

The classic case of so-called "double adaptation" in *Polygonum amphibium* which is pubescent in its terrestrial form and glabrous when grown as an aquatic, and other cases of the same kind, present illustrations of latency due to fluctuation, instead of being due to the presence of two antagonistic determinants whose activities are mutually exclusive as suggested by De Vries.[12]

The very common occurrence of latency due to fluctuation must have an important bearing upon the significance of cultural conditions for the production of variations. There has been much diversity of opinion on this point, the general impression being that cultivation and the removal of competition are very potent in inducing

[12] De Vries, H. Species and Varieties, their origin by mutation, pp. xviii + 847. 1905. Chicago: Open Court Pub. Co. See p. 430 *et seq.*

[11] Lock, R. H. Plant Breeding in the Tropics. III. Experiments with maize. *Ann. Roy. Bot. Gard. Peradeniya*, 3, pt. 2, pp. 95–184, November, 1906. See pp. 144–163.

variation, and that in consequence of this fact it is improper to apply principles derived under cultivation to plants growing free in nature. There can be no doubt that good cultural conditions render patent many internal characters which are invisible under conditions of poor nutrition and crowding, and this fact together with the fact that many of the common culture-plants are complex hybrids, may fully account for the general impression regarding the effects of culture. There is no satisfactory evidence that good feeding and other conditions usually supplied under tillage have any effect in the production of the mutations upon which the external characters no doubt ultimately depend.

General Considerations

It is obvious from the foregoing results and discussions that latency is not a simple phenomenon, but may be due to a number of different circumstances. The point which I have strongly emphasized in my two preceding papers on the subject of latency—namely, that cases of latency must be explained, not upon the ground of inactivity or dormancy of characteristics, but simply on their invisibility— is fully borne out by all the facts here presented. The several different types depend upon the different causes for the invisibility of the characteristics.

Of the four types of latency here recognized, the first three types—those in which latency is due to definite interrelations between Mendelian units—will give rise to definite characteristic ratios which are as constant for each case as the typical ratios are for typical Mendelian phenomena. This is not so with latency due to fluctuation, as the variable conditions upon which the fluctuations depend may be such that any proportion of the individuals from none to all may have the character in question latent. This is not only true of the characters of pure-bred types as exemplified by *Bursa bursa-pastoris*, but is even more apt to be true of heterozygotes, thus resulting in many deviations from the correct ratios, as

seen in Lock's blue × white corn cross and doubtless in very many other cases.

It is probable that many discrepancies between actual and theoretical ratios are due to some sort of latency. This will generally be detected readily in subsequent generations, and no one should be hasty in declaring that a character which is of the splitting kind is non-Mendelian until the various types of latency are considered which may have taken part in modifying the ratios. "Variable potency," "contamination" or "impurity" of the gametes, and "alternating dominance" will all need to be reconsidered and in some cases reinvestigated, before they can have any secure standing as exceptions, amendments or additions to the simple law of "purity of the gametes" which is the essence of Mendelism.

There is still another way in which unexpected ratios may be produced, without in any way affecting the fundamental principle of the purity of the gametes, their production in equal numbers, and their union according to the laws of chance, and while the question of latency is not involved in this case, it deserves to be mentioned in this connection. Baur[13] has shown that in a variegated race of Antirrhinum, the variegation belongs only to the heterozygote. The extracted recessives are green and the extracted dominants fail altogether to appear, owing evidently to the fact that the zygote so formed is incapable of development, the ratio resulting from self-fertilization of the heterozygotes being therefore 2:1. It is conceivable that every degree of inefficiency of zygotes formed by the union of two particular allelomorphs might occur and thus quite various modifications of the expected ratios be the result, when those ratios are determined by a count of the successful zygotes. This cause for the failure of the expected ratios is certainly of rare occurrence, but like questions of latency it can be demonstrated

[13] Baur, E. Untersuchungen über die Erblichkeitsverhältnisse einer nur in Bastardform lebensfähigen Sippe von *Antirrhinum majus*. *Ber. Deutsch. Bot. Gesell.*, 25, pp. 442–454, 1907.

without difficulty by breeding tests, and these should be made before any new principle is invoked, or the old and well-founded principles are declared invalid, in the attempt to account for such discrepancies.

SUMMARY

The foregoing discussion and conclusions may be summarized thus:

In certain bean hybrids, mottled seed-coats depend upon the presence of a mottling allelomorph in a heterozygous condition, the homozygous condition giving unmottled seeds. This peculiar situation results in a tripolyhybrid ratio, 18:18:6:6:16, instead of the usual ratio, 27:9:9:3:16.

Latency is held to mean invisibility, and not inactivity or dormancy, and four types are recognized, according to the different causes of invisibility; still other types may be found. The four types discussed in this paper are:

(*a*) *Latency due to separation,* in which an allelomorph when acting alone has no external manifestation and is only rendered patent by combining it with another allelomorph. Such latency gives rise to the ratios 9:3:4, 9:7, 27:9:9:3:16 and 27:9:28, instead of the theoretical, 9:3:3:1 and 27:9:9:9:3:3:3:1.

(*b*) *Latency due to combination,* in which two dominant allelomorphs, each giving rise to a peculiar character when acting alone, lose their external manifestation when co-existing in the same zygote. Upon self-fertilization this type of latency gives rise to such ratios as 1:1, 3:3:2, 18:18:6:6:16, etc., and may be found to account for the existence of certain mid-races, and other cases in which a double series of characteristics are presented in nearly equal numbers.

(*c*) *Latency due to hypostasis,* in which the presence of one allelomorph can not be detected owing to the presence of another allelomorph, the character produced by the latter being unmodified by the activity of the former. This type of latency is exemplified by the black bean

which hides the presence of a wholly distinct brown allelomorph, and a dark orange bean which carries invisibly a light yellow allelomorph. This condition gives rise in one series of crosses to the ratio, 12:3:1. Properly the term "dominance" should be limited to the relation between any positive characteristic and its own absence. Whenever one positive character seems to dominate another positive character, the latter is latent by hypostasis in the individual possessing the former.

(*d*) *Latency due to fluctuation,* a very frequent phenomenon in which characteristics disappear under conditions of poor nutrition, etc. Cultivation under favorable conditions makes such characteristics patent and this fact may account in part for the general impression that cultivation induces variation. Cases of "double adaptation" are examples of this type of latency.

Many discrepancies between theoretical and empirical inheritance-ratios are due to latency, and care should be taken to investigate the possible latencies which may be present before declaring that a character is non-Mendelian, because of a discrepant ratio. "Variable potency," "contamination" or "impurity" of the gametes, and "alternating dominance" which have been proposed to account for the appearance of various novelties, or of deviations from expected ratios, can have no secure standing until the question of latency in the sense of invisibility has been taken into account.

A modification of expected ratios may rarely result also from the failure of certain allelomorphs to make vigorous zygotes when joined together in certain combinations.

THE LEG TENDONS OF INSECTS

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WHILE perhaps known to working morphologists, the fact that the leg tendons are cuticular invaginations, and therefore subject to replacement at each molt, does not appear to have attracted the attention of any of the writers of text-books, and as far as the writer of this article is aware, has not been published at all.

The three best developed tendons are the two operating the knee joint and the one that flexes the claws. These three are almost invariably present, though one or the other may be very short, or present only as a cuticular thickening.

These structures are very easy to study in small insects. I have found aphids the most satisfactory subjects. The legs of most species are transparent enough to show the structures well when mounted whole, and the exuviæ are especially satisfactory objects. They may also be obtained in such abundance that one can mount large series of specimens, thus obtaining mounts showing the legs from almost any desired point of view.

The knee joints provide for the largest amount of motion of any of the joints of the leg, and this motion is all maintained in one plane by the development of two bearing points, making a hinge. The end of the tibia is small enough to telescope within the femur but for these articular processes. They consist of a process projecting inwardly on either side of the rim of the femur, as shown in Fig. 1, *A* and *B*, and corresponding with these femoral processes there are slight outwardly projecting processes from the margin of the thickened rim of the tibia. The articular membrane at these points prevents the displacement of the processes.

The whole dorsal end of the tibia, including these processes, is very largely hardened and thickened and marked off from the body of the tibia by a deeply infolded ridge. Most of this thickened portion is within the end

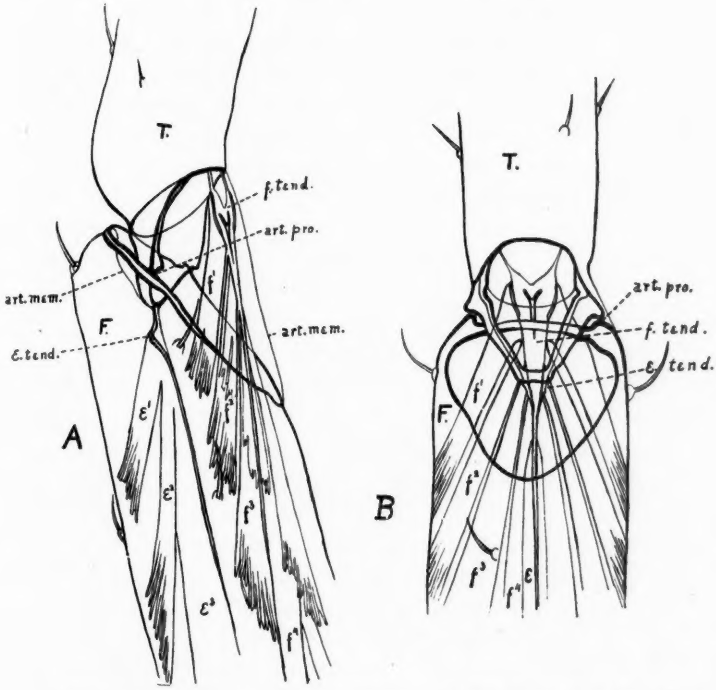

FIG. 1. The knee joint of *Aphis brassicæ*. *A*, side view; *B*, viewed from beneath; *T*, tibia; *F*, femur; *art.pro*, articular process; *e.tend*, extensor tendon; $e^1e^2e^3$, extensor muscles; *f.tend*, flexor tendon; $f^1f^2f^3f^4$, flexor muscles; *art.mem*, articular membrane.

of the femur when the leg is fully extended, but is all exposed when the leg is at extreme flexion. An articular membrane connects the extreme edges of femur and tibia, as shown in Fig. 1, *A*.

Beneath, the hard parts of both femur and tibia are deeply emarginated, exposing a broad articular membrane. When in extreme flexion the rims of tibia and

femur almost touch, and the articular membrane is drawn deep into the femoral cavity. The tendons find their attachment to the outer and inner sides of the rim of the tibia and, extending into the cavity of the femur, serve for the attachment of a series of muscles, as shown in Fig. 1, *A* and *B*.

The flexor tendon in the earlier stages is only a V-shaped thickening of the articular membrane, but later the point of the V extends deeply as an internal pocket for the attachment of muscles reaching nearly to the base of the femur. There are two sets of muscles attached to this tendon, extending obliquely to the right and left sides of the femur. The first of these, f^1, in the figures lying at about 45° to the long axis of the femur, and the others marked f^2, f^3, etc., lying more nearly longitudinally.

The extensor tendon attaches to the dorsal rim of the tibia by a broad ribbon-like portion and soon expands into a broad plate at right angles to this first portion and then

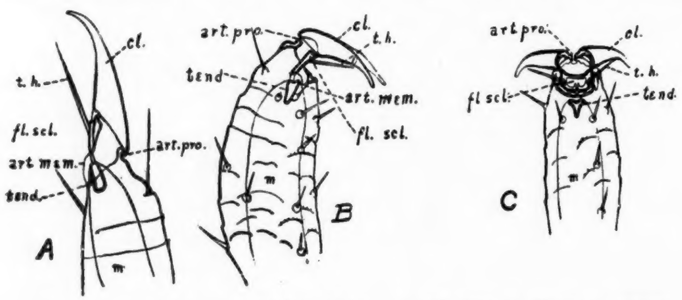

FIG. 2. End of foot of *Aphis brassicæ*. *a*, side view of claws at extreme extension; *b*, *Ibid*, claws flexed; *c*, viewed from beneath; *cl*, claw; *t.h*, tactile hair; *fl.scl*, floating sclerite; *art.pro*, articular process; *art.mem*, articular membrane; *tend*, tendon; *m*, muscle.

narrows to a ribbon and extends deeply into the femur even in the earliest stages. A short muscle, *e*, is attached to the disk, followed by a series of others, somewhat as the flexor muscles are arranged, only that there is but a single series, finding their attachment to the middle dorsal side of the femur. Tendons are first developed as somewhat tubular processes, but always collapse after the

molt so that the tubular character can never be made out. In the case of the extensor tendon of the knee the enlarged disk must require a considerable stretching of the portion of the tendon further out to enable it to pass.

The tendon of the claw is very short up to the last molt in the case of plant lice. The structure at the end of the last tarsal joint is shown in Fig. 2. At the extreme end of the foot there are two processes over which the base of the claws rotate. The only other attachment aside from the soft articular membrane is a median floating sclerite capping the larger part of the end of the cavity of the foot and which bears the tactile spines extending forward below the claws. This floating sclerite in other insects forms the base of the empodium and pulvillæ. Neither of these is present in the case of the plant lice unless the soft skin immediately beyond this sclerite be so designated. The lower edge of the margin of the cavity is a strongly developed ridge upon which the internal tendon bears when the claws are extended, and against which the floating sclerite rests in extreme flexion. On either side of this thickened and elevated ridge there is a distinct notch allowing considerable lateral motion of the sclerite. The posterior ridge of this floating sclerite extends inward as two processes joining with the two wings of the heart-shaped tendon. The tendon proper is entirely internal as is shown in the figure, and the muscle fibers are attached to all sides. The other attachment of the muscle is to the base of this large second joint of the tarsus.

There are really no true tendons in insects; *i. e.,* the tendons of the legs are only such in a physiological or morphological sense, and not at all in structure or origin, but belong instead to the class of internal processes which includes the well-known internal skeleton or the head and thorax, the tendons of the jaws in mandibulate insects, the great internal disk-like tendons for the attachment of the elevator muscles of the wings in the Odonata, and the skeletal and tendonal process of the ovipositor. The

only difference between a skeletal process and a tendon is that one is invaginated from a relatively fixed part of the body and the other from a moving part. While insect tendons are, therefore, not homologous with the tendons of vertebrates, it is probably wise to retain the name just as in the case of femur and tibia for parts of the leg, where likewise there is no homology with the bones of vertebrates where the names primarily apply.

ABNORMAL INCISORS OF MARMOTA MONAX L.

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The common woodchuck or ground hog, *Marmota monax,* is found rather frequently in most parts of central Kentucky; and, since it occupies the same burrows, or others in the immediate vicinity, generation after generation, it is not uncommon to find in these regions portions of their skeletons, skulls, vertebræ, teeth, etc., in the neighborhood of their habitations.

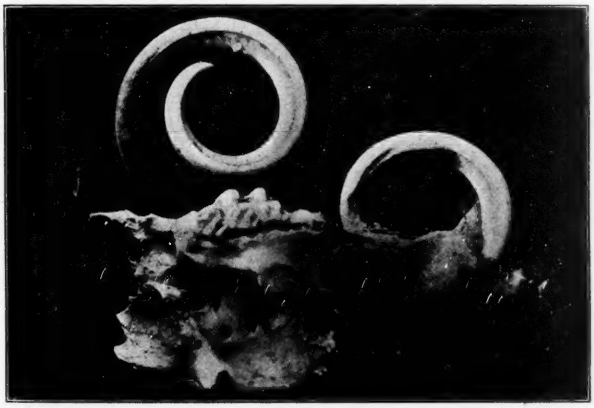

Fig. 1. Skull of *Marmota monax* L., right incisor removed. Natural size. Photograph by Spengler, Lexington, Ky.

The interesting specimen which is illustrated here was found near Silver Creek, Madison Co., Ky., by Mr. Charles Meeks, who presented it to Mr. Thomas Goff, of Lexington, Ky. It has recently been given to the Museum of Transylvania University. The upper incisors are extremely long and curved so as to form with the parts imbedded in the premaxilla more than a complete

circle. This is beautifully illustrated by Fig. 1, in which the right incisor has been removed from the jaw.

Both teeth are turned somewhat toward the right, so that the right one projects from the mouth; but the left incisor strikes the roof of the mouth to the right of the median suture, piercing the palatine plate of the maxilla

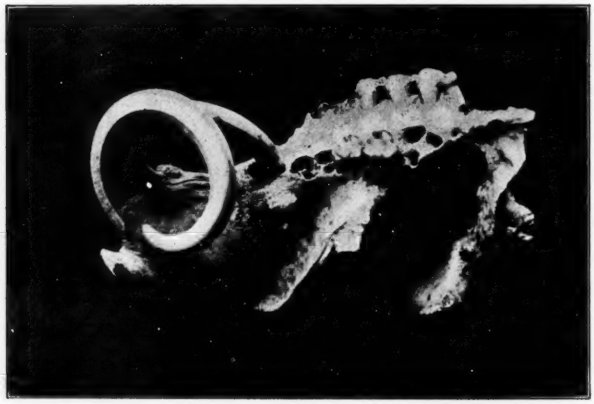

FIG. 2. Skull of *M. monax* L., with left incisor piercing palatine plate of right maxilla. Natural size. Photograph by Spengler, Lexington, Ky.

(Fig. 2) and extending through it to a distance of about 5 mm. The left tooth is not as long as the right one, its growth having been retarded, perhaps by the hardness of the bone it penetrated.

The manner in which the teeth of *Marmota monax* grow is familiar to all who know the Rodentia. The rodents all have a diphyodont dentition, that is, there are two sets of teeth, a temporary or deciduous set, and a permanent set. But the permanent teeth never cease to grow. There is a persistent pulp at the base of each tooth, which grows throughout the life of the individual.

Ordinarily the corresponding teeth of the upper and lower jaw oppose each other perfectly, and the growth from the pulp only compensates for the amount worn off by biting. The incisors have a heavier coat of enamel on

the anterior portion of the tooth, and the more rapid wearing of the posterior edge keeps these front teeth chisel-like and sharp.

The abnormal growth of the incisors will occur whenever the upper and lower teeth fail to meet. An injury to either jaw, as for instance a bullet wound, might destroy the perfect opposition of the incisors. But the teeth in this specimen are sharp pointed and not worn at the distal end, as they would be if they had ever functioned properly, which fact would indicate that the wound must have occurred before the permanent teeth appeared.

A careful examination shows that the abnormality can be accounted for in another way. The socket of the left incisor is not normal in its position, and the tooth itself grows inward toward the right incisor, striking it about 8 mm. from the jaw. The latter tooth has on its inner side a groove extending from near the distal end to the point where the two incisors are in contact. This groove was produced by the pressure of the left incisor upon the right, and this pressure is undoubtedly the cause of the failure of both teeth to meet the lower ones. The abnormal growth then depended primarily upon a congenital abnormality in the position and direction of the socket of the left incisor. One of the lower teeth of the same skull was found, but has been misplaced. Mr. Goff informs me that it also was curved and much longer than usual.

It would be of interest to know how the animal with this curious set of teeth obtained food sufficient to prevent starvation. It may well be that this abnormality was the chief determining factor in its struggle for existence.

A NOTE ON THE COLORATION OF PLETHODON CINEREUS

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On September 9, 1905, Mr. A. A. Allen found, near Buffalo, N. Y., a salamander[1] 6.5 cm. long which was, at first sight, believed to be a small *Spelerpes ruber,* but closer inspection proved it to be otherwise. The head, sides and back are of uniform coral red, gradually fading into pinkish on the immaculate belly (Fig. 7). The sides and the dorsum of the distal half of the tail are heavily mottled with black, leaving the dorsal line of the proximal half the same color as the body. The mottling extends upon the ventral side of the tail, but the spots are here much lighter so that the general pink color of the under parts is evident. On the right side the black blotches of the tail begin immediately behind the leg, while on the left the base of the tail is an immaculate red for some distance behind the leg.

This specimen was found under a piece of bark in a dry and rather open woodland. About three weeks later in a nearby locality there was found a second specimen which upon comparison proved to agree in all essential respects of coloration with the first. This one escaped before it was killed and preserved.

On April 27, 1907, near Beesemer, N. Y., a short distance south of Ithaca, Mr. Allen found another specimen[2] (Fig. 6) which is identical in form and similar in coloration to those taken near Buffalo. The Beesemer specimen is a carrot red with a cluster of minute black dots on the top of the head and a row of similar dots along the sides of the back in a position which corre-

[1] No. 5,047 Cornell University collection.
[2] No. 5,048 Cornell University collection.

sponds to the dorsal portion of the black lateral band in *Plethodon cinereus erythronotus.* This row of dots is broadest above the region of the arm, whence it is gradually reduced as the leg is approached. The coloration of the tail is similar to that of the Buffalo specimen excepting that the black color, instead of being collected in blotches, is more diffuse and continuous with the same color in the trunk region.

When these specimens were examined more closely they were found to have the body proportions and all of the structural features of *Plethodon cinereus.*

In the Cayuga Lake Basin both *Plethodon cinereus cinereus* and *P. c. erythronotus* are abundant and great variation with regard to coloration has already been noted. Several hundred specimens, mostly from this region, were examined with a view to determining the extent of the variation in coloration. This resulted in the selection of a series of fifteen individuals, of practically the same size, which show a fairly complete transition, in regard to coloration, between the typical *Plethodon cinereus cinereus* and the red forms taken near Buffalo. The middle of the series is occupied by a typical *P. c. erythronotus* (Fig. 4). From this variety the coloration in one direction grades into *P. c. cinereus* and in the other into the red form.

Cope[3] describes the variety *erythronotus* as follows:

"A broad light-reddish stripe commences at the nape of the width of the interorbital space, and continues to the tip of the tail, on which it diminishes gradually in width. The central region of the stripe generally exhibits a very fine mottling of brownish, scarcely obscuring the effect of the red ground. The mottling is sometimes equally distributed—sometimes concentrated in some places more than others. The sides of the body are abruptly and continuously dark brown, but soon fade off below into the pepper and salt of the lower sides and belly. . . . The color of the red stripe varies considerably. Sometimes it has a shade of pink—sometimes of orange or yellowish."

In all individuals examined from this region the red dorsal stripe on the tail grows narrow very rapidly. The

[3] Cope, E. D., "The Batrachia of North America," Bull. 34, U. S. Nat. Mus., p. 135.

distal third is mottled so heavily with black that the stripe, as such, is lost. The large number of specimens examined indicates that the typical *P. c. erythronotus* is not more common here than the red intermediates.

The transition between the variety *erythronotus* and the red form is accomplished thus: the red dorsal stripe first extends cephalad covering the whole top of the head where there is found in all intermediates a sprinkling of brown dots (Fig. 5). It then invades the sides of the head passing to the snout underneath the eyes. From this position it spreads in all directions, replacing the brown until the whole body is thoroughly suffused with red. In such specimens the brown color-pattern is evident but subdued by the red tone due to the invasion of this color into the whitish areas between the clusters of brown blotches.

The further transition consists in the expansion of the red ground-color and the gradual reduction of the brown blotches which persist longest on the top of the head, along the dorsal abrupt border of the lateral band, down the middle of the back and on the tail. In the Beesemer specimen only the vestiges of the brown markings remain in the regions just mentioned. On the limbs the invasion of red proceeds from the base towards the extremity, the brown markings showing longest upon the hands and feet.

In the Buffalo specimen the brown markings are everywhere apparently obliterated excepting upon the tail, the snout and the region between the eyes and a cluster just behind and below the left eye. In the alcoholic specimen there are revealed, along the sides of the back in the shoulder region, very fine specks of brown pigment arranged in a narrow band which can be traced to the leg region, although the dots are faint and much scattered in the caudal half, and in the living specimen did not show at all.

According to Cope[4] intermediate specimens between

[4] Cope, *op. cit.*, p. 136.

the varieties *erythronotus* and *cinereus* are uncommon, for he says:

"Among the very great numbers of specimens which I have examined in the collections of the Smithsonian Institution, The Academy of Natural Sciences and Essex Institute I have observed but four specimens of the red-banded variety and four of the gray which could be regarded as intermediate in character."

In the material at hand I find that the intermediate individuals, between the varieties just named, are fairly numerous; so that a series was selected which forms almost an insensible transition from the one to the other. The method here is exactly the reverse of that described above in connection with the red forms; *i. e.*, the red is replaced by brown. In describing the intermediate specimens which he studied, Cope outlined the method which I find carried out in detail in my material. He writes:

"This [the intermediate character of his specimens] appears in a rufous cast in the dorsal color of the latter [variety *cinereus*] and a slight obliteration of the borders of the dorsal band in the former [variety *erythronotus*]."

The brown of the lateral band in *P. c. erythronotus* begins first to encroach upon the red of the dorsal stripe so that its edges become scalloped (Fig. 3). This spreading of the brown color continues until the dorsal stripe is heavily blotched and the red becomes very dull (Fig. 2). Then the brown blotches gradually coalesce, in consequence of which the red stripe, as such, is obliterated, yet enough of the red pigment remains to give the effect of a dull liver-brown to the back of *P. c. cinereus*. In a number of specimens of this variety all traces of liver-brown have disappeared, rendering the back uniform in coloration with that of the sides (Fig. 1).

In respect to structural characteristics no variations were detected except in the case of one red intermediate where only seventeen costal grooves were present. The body proportions of this individual were slightly less than the others.

Data bearing upon the relation of this variation to environment, food, moisture, etc., are entirely wanting. The red specimen taken near Buffalo was at an altitude of 1,000 feet above sea level. That near Beesemer, 800 feet. Individuals kept in the terrarium under entirely different conditions than those from which they were taken in nature never change in coloration so far as I can determine, which indicates that the variation is independent of the nervous system. The age of the individual seems to have no relation to variation. Among adults of all sizes the different intermediate forms are found. There are in the collection of Cornell University about a dozen specimens taken soon after transformation. They are all typically of either the variety cinereus or erythronotus except one which varies decidedly towards the red form.

EXPLANATION OF PLATE.

FIG. 1. *Plethodon cinereus cinereus* in which all traces of the dorsal stripe have disappeared.
" 4. *Plethodon cinereus erythronotus.*
" 6. The red specimen taken near Beesemer, N. Y.
" 7. The red specimen taken near Buffalo, N. Y.

The other figures, according to their position, are intermediates between *P. c. cinereus, P. c. erythronotus* and the red Buffalo specimen.

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A.G. Hammar, del.

SOME EXPERIMENTS ON THE ORDER OF SUCCESSION OF THE SOMITES IN THE CHICK

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THE experiments described in the present paper were performed at the University of Chicago during the year 1903–04, under the direction of Professor F. R. Lillie, to whom thanks are due for much advice and suggestion. In the course of the preparation of the data for publication during the last summer I learned that another investigator, Mr. J. Thos. Patterson ('07), had hit upon the same problem, and his results appeared before this article could be published. It has been suggested, however, that the work described may be of value in confirming Mr. Patterson's conclusions.

The problem, suggested by Professor Lillie, was the investigation of the statement, so generally made by embryologists, that, in the chick, somites arise in front of the one which is formed first. An examination of the most important of these statements will make clearer the nature of the problem. The estimates of von Baer ('28) and His ('68) did not require serious consideration, for they were not based upon a close study of this point. That of Kupffer and Benecke ('79), who thought that three or four somites arose in front of the one which first appeared, was founded upon an examination of a rather wide series of embryos, but only in surface view. Miss Platt's ('89) work rested upon a study of sagittal sections, and as it was altogether a careful examination of the subject, my attention was directed particularly to her conclusions. Briefly, her account of the formation of the somites is as follows:[1] The first cleft divides two

[1] *Loc. cit.*, pp. 177, 178.

forming somites. The somite behind the cleft is called the first one in the series. The one anterior to it, protovertebra *a*, forms slowly, while four or five are making their appearance behind. After five or six somites are visible in all, another, protovertebra *b*, arises slowly in front of *a*. Protovertebra *b* is said to be rudimentary, never becoming completely cut off from the mesoderm in front.

It will be noted in this account that although two somites are described as arising in front of the one first formed, in reality there is but one to be considered—protovertebra *b*—for protovertebra *a* makes its appearance at the same time with the one behind it. An examination of Miss Platt's sections[2] would lead one to agree in the main with her account of the order of formation of the somites, except in regard to the appearance of protovertebra *b*, whose growth has to be followed in a series of sections from different embryos at successively older stages. The difficulty of identifying a growing somite in this way casts much doubt upon even its existence, and it was to test the question therefore that these experiments were devised.

The aim of the experiments was to mark or destroy, in embryos with a small number of somites (not more than five or six) the most anterior somite on one side, and so to determine whether any more were later formed in front of this. The ideal stage to have secured would have been that of an embryo with only a single pair of somites, but repeated failures to obtain this condition verified the statement made by Miss Platt,[3] founded upon a study of sections, that the first cleft occurs between two forming somites. An operation, then, even as early as at the time of the first cleft would have had to take into account the first two pairs of protovertebræ.

The methods employed in the experiments were in general similar to those used by Mr. Patterson. For open-

[2] *Loc. cit.*, Plate I.
[3] *Loc cit.*, p. 177.

ing and sealing the egg Miss Peebles'[4] method was followed. For destroying the somites two fine depilatory needles, ground to a hair point on an oil-stone, were used, one, at the negative electrode, touching the albumen, the other, at the positive electrode, serving to prick the somite which was to be marked or destroyed. For the current four Samson dry-battery cells, each with an electromotive force of 1.5 volts, were connected in series. To prevent infection the instruments were sterilized in a flame. With this method of disinfection, 15 out of 84 embryos, or 18 per cent., were lost, but as the loss was occasioned by the sticking of the blastoderm to the shell, it can not be stated that it was not due in part to causes other than bacterial infection. A Zeiss dissecting stand was used for the operations, with lenses magnifying six diameters, and whenever possible the work was done with the bright sunlight shining in upon the blastoderm. So great is the variation in distinctness of embryos at this early age, that even with the best of light the somites could not, except in a comparatively small number of cases, be counted with certainty. In the embryos, however, which were distinct, there was no room for doubt as to their exact condition at the time of the operation.

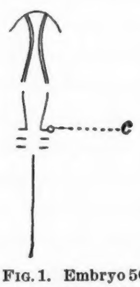

FIG. 1. Embryo 50. Sketch made at time of operation. c = place of operation.

From several experiments, the results of which furnish evidence for the solution of the problem, the following case has been selected for description:

Number 50 was operated upon after 30 hours of incubation. The operation was performed with the sun shining in upon the blastoderm, the embryo was distinct, and its three somites were readily counted. Fig. 1 is a sketch made at the time, showing the place of the operation, in which, it was noted, the needle passed obliquely inward.

[4] *Loc. cit.*, p. 406.

Fig. 2 shows the same embryo after nineteen more hours of incubation. The heart was beating when the egg was opened. The embryo was preserved in picrosulphuric-acetic acid, stained in Conklin's picro-hæmatoxylin, and mounted in xylol balsam. The drawing was made with the aid of the Abbe camera.

The first right somite is noticeably smaller than its fellow on the left, there is no break between it and the mesoderm in front, and only the posterior part of it shows the radial arrangement of cells which is characteristic of the normal somite. The scar of the operation shows at the side. A deeper examination in this region reveals, mediad of the scar, a clear area extending into the limits of both the first and the second somite of that side, indicating that the injury reached inward from the point of entrance of the needle. The second somite is also incomplete on its dorsal antero-lateral corner, as shown in the figure. Except for these injuries and the bend to the right which may have been caused by the operation, the embryo appears normal, the break in the neural tube at the anterior end being the result of pressure of the cover-glass.

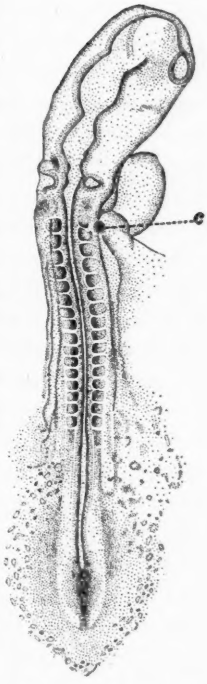

FIG. 2. Embryo 50, incubated 19 hours after operation. c = scar of operation. ×20.

Whatever else this experiment proved, it showed clearly that not more than two somites could arise in front of the one which is first formed. This of course shut out at once the hypothesis of Kupffer and Benecke, who assumed that three or four somites are probably formed in front.

Applying Miss Platt's description of the order of ap-

pearance of the somites to this case, it would seem that this embryo must have had the first of the two anterior somites, protovertebra *a*, already partly formed, at the time of the operation, and that there should, therefore, have been one more, protovertebra *b*, to arise in front of this. But no such somite appears in Fig. 2, and its absence led to the conclusion that there is no such somite as protovertebra *b*, in other words, that but one somite is formed in front of the first cleft which appears. The simplest explanation of Miss Platt's error is that she mistook protovertebra *a* in sections of older embryos for protovertebra *b*. This is much more probable than that she could have mistaken, as Mr. Patterson suggests,[5] the most posterior transitory shallow depression in the head mesoderm for the first cleft.

If it be objected that the experiment does not prove that one or two somites may not arise in front of the one first formed, it may be said that if they do arise, the rate of their formation, compared with the rate of formation of those that appear behind, is contrary to the description of this process by Miss Platt,[6] according to whom the rate of formation is much greater behind the first formed somite than it is in front. Either then somites are not formed in front, or, if they do arise, the description of the rate of their formation is not correct.

In conclusion, then, this experiment, in proving that not more than two somites could arise in front, showed the inaccuracy of Kupffer and Benecke's estimate of the number formed.

It showed further, in regard to Miss Platt's work, either that her description of the time of formation of the somites was incorrect, or, if development proceeds according to her account, that no somites, except the rudimentary one, arise in front of the first cleft.

Thus the result of the experiments, with reference to the condition of the problem up to the time when Mr.

[5] *Loc. cit.*, pp. 129, 132.

[6] *Loc. cit.*, p. 177.

Patterson began his work upon it, was to throw the burden of proof on those who claimed that somites do arise in front of the one first formed, rather than on those who held that, in their formation, they obey the laws of progressive differentiation which govern the early development of birds.

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DWARF FAUNAS

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Faunas in which all the individuals are uniformly so small as to be notable for this reason are common both in recent and past times. Such dwarf faunas may be merely an association of normally small species; or they may be individuals much smaller than the normal size for that species, prevented for some reason from attaining full size.

The following is an attempt to summarize some of the principal recent and dwarf faunas with the probable causes producing them. It is confined to invertebrate, water-living faunas. The article is primarily a summary of such literature as chanced to be seen; that very much of importance was overlooked is undoubtedly true, but it is thought that the major causes of dwarfing are here noted.

The first part of the article is a discussion of the chief agencies of dwarfing using recent examples as illustrations; the second part considers a few fossil examples of dwarf faunas with their probable causes.

The following are the chief agencies of dwarfing as noted in recent and fossil faunas:

1. A change in the normal chemical content of the water.
   - (*a*) Due to a freshening of the sea water.
   - (*b*) Due to a concentration of the salt, iron, etc.
   - (*c*) Due to an increase in H_2S and other gases.
2. Presence of mud and other mechanical impurities in the water.
3. A floating habitat.
4. Variations in temperature.
5. Extremes in depth of water.

1. *A Change in the Normal Chemical Content of the Water.*—Any change in the environment of an animal which is away from that best suited to its highest development tends to its deterioration. If a species develops best in normal sea water, then an increase or decrease in the chemical content of the water should be detrimental to the animal, and this detriment should be expressed in the shell, since, as shown by Hyatt and others, there is the most intimate relation betwen the soft and the hard parts of an animal, the least injury in the soft parts being immediately expressed in the growing shell. This expression will usually take the form of a dwarfing in size, thinning and smoothing of the shell or development of bizarre form.

The possible changes in the normal chemical content of the water are exceedingly numerous and all doubtless affect the animal to a greater or less degree. The following appear to be some of the more important of such changes which produce a dwarfing effect.

(*a*) *A Change due to Freshening of the Water.*—That many forms of animals find fresh water detrimental to them appears to be indicated by the fact that at present whole groups are excluded from it, as the Echinodermata, Brachiopoda, Cephalopoda, Tunicata, etc.

The many streams emptying into the Black and Caspian seas, make them fresher than the Atlantic Ocean. The faunas of these are typically marine, but practically all are dwarfed in size as compared with the same species in the Atlantic. For example, the following Black Sea species are considerably smaller in the Black Sea than in the British seas: *Littorina rudis, Cerithium adversum, Trochus umbilicus, Murex erinaceus, Nassa reticulata, Cardium edule, Anomia ephippium, Venus gallina, Tellina tenuis, Mactra triangula, Solen ensis, Pholas candida,* etc.[1]

The common European cockles, Cardium, are large, thick and rough shells, and thrive best under purely marine conditions. The species found growing in brack-

[1] Forbes, E. Nat. Hist. of European Seas, pp. 201 and 202.

ish waters are smaller than those in normal sea water. *Cardium edule* is found in the British Isles in harbors and high up tidal rivers, where the water gets brackish; its shell is modified, invariably reduced in size, thin, and with less strongly marked external characters. The ten species of Cardium in the Caspian Sea are all aberrant forms, all related back to *C. edule,* small, thin and smooth, with lateral or central teeth or both suppressed. So likewise with the cockles of the Black and Baltic Seas; in the latter the salinity is reduced one half by the water from the rivers.[2] The Greenland cockle lives in estuaries; it is no longer found in Europe but is very abundant in the Pliocene (Crag) of Suffolk and Norfolk, especially in the fluvio-marine portions. It is thin, smooth, almost edentulous, with rudiments of a single tooth in each valve in the young shells which finally disappear.[3]

Some forms, as Scrobicularia and *Mactra solida,* have become thoroughly adapted to a brackish water environment and attain their largest size there. But many, if not most species, which live in normal sea water and in brackish water are smaller in the latter, as is true of *Cardium edule, Mya arenaria* and *Littorina littorea.*

(*b*) *Change due to a Concentration of Salt, Iron, etc.*—When a body of water has become concentrated to a point where precipitation of its salt takes place, as is practically the case in the Great Salt Lake or entirely so in the Dead Sea, no life can exist in it. But from the normal sea water to this condition there takes place progressively a lessening both in the number of species and in the size of the individuals there present.

Many fossil dwarf faunas have been ascribed to this cause, as, for example, those of the Permian.

That even a comparatively slight concentration of the sea water may produce a dwarfing in its fauna appears to be indicated by the western Mediterranean species. Dana gives the amount of saline matter in the Mediterranean as 3.9 per cent. as against 3.6 per cent. for the

[2] Dana. Manual of Geology, p. 121.

[3] Forbes, E. *Loc. cit.*, pp. 211–215.

Atlantic.[4] De Lapparent[5] states that this western portion has a few of the Atlantic species but all of reduced size. A comparison of British and Spanish coast species gives the same result. *Haliotis tuberculatus*[6] is larger at Guernsey than on the Spanish coast. The difference of temperature between the two localities may be another factor in causing this dwarfing.

(*c*) *Change due to an Increase of* H_2S.—The presence of much of this heavy gas in an enclosed or partially enclosed basin would prevent the presence of living organisms and hence the only fauna which sediments deposited here could contain, would be free-swimming or floating individuals. This pelagic fauna contains besides fish, pteropods, and especially larval forms of almost every animal group. Thus the sediment of such an enclosed basin would contain small shells, embryonic in character, pteropods and a few fish. Andrussow[7] has shown that in consequence of the greater salinity and density of the deep water, the Black Sea shows only slight evidence of vertical currents. Such currents are apparent only to a depth of 125 fathoms, and hence only to this depth is there sufficient oxygen for the support of animal life. At a depth of 100 fathoms the separation of H_2S is observable, increasing in amount with the increase in depth. The separation of H_2S is regarded as due to the agency of microbes (Sulfobacteria) living upon animal remains of the free-swimming and floating forms of life sunk to the bottom. It is attributable in part also to the derivation from sulfates. Hand in hand with the separation and enrichment in H_2S is the diminution in sulfates in the sea water, the separation of the carbonates and of FeS. In the great depths of this sea the bottom is covered with black or dark blue mud in which are abundant remains of free-floating diatoms, fragments of quite young pelecypods, and minute grains of $CaCO_3$, and much FeS.

[7] Clarke. N. Y. State Mus. Mem., 6, 200.

[4] Manual of Geology, 4th ed., p. 121.

[5] Traite de Geologie, 5th ed., 1, 132.

[6] Forbes. *Loc. cit.*, p. 171.

2. *Influence of Mud and other Mechanical Impurities in the Water.*—Though the western Mediterranean contains a dwarf fauna, yet it is the eastern part which is especially so characterized. This is attributed by de Lapparent[8] to the presence in the water of the eastern basin of many very fine particles of solid matter (Nile sediment) which becomes deposited only very slowly. A similar cause apparently aided in dwarfing some of the faunas of the Windsor (Nova Scotia) Carboniferous, also those of the Cobleskill, Rondout, Manlius, Bertie, etc.

3. *Influence of a Floating Habitat.*—Forms which live attached to floating seaweed will tend to be small owing to the fact that the increased weight of the individual due to growth will cause its sinking with its attached seaweed before the attainment of large size. Hence only the smaller individuals would occur on the seaweed or in the sediment beneath. Fuchs has shown[9] that in the eastern, shallower part of the harbor of Messina, the sea is now filled with different kinds of algæ, densely crowded together. This seaweed thicket swarms with small mollusks, seeking here food and protection. Here are species of Rissoa, Trochus, Turbonella, Columbella, Marginella, Cerithium, Cardium, Cardita, Lucina, Arca and Venus, but they are throughout of smaller size than normal. This dwarf fauna is thus not the result of stunted growth but is very probably due to the fact that the algæ can not support large and heavy shells. Such dwarfing and also thinning of shells fastened to seaweed (giant kelp) Arnold[10] notes in the case of *Pecten latiauritus* var. *fucicolus* of the California coast. This in its floating habitat far from shore is not subjected to the shock of the breakers, and hence the shell not only remains thin but also gradually loses its ribbed ornamentation. *P. latiauritus* likewise grows attached to kelp but when near shore it is more strongly sculptured than when living in deeper and quieter waters.

[8] *Loc. cit.*, 5th ed., 1, 132.
[9] Walther. Einleitung in die Geologie, p. 33.
[10] U. S. G. S. Prof. Paper 47, p. 131.

The ability of mollusks to reproduce before the attainment of full size accounts for the perpetuity of such dwarfed species. Semper, in reference to oysters and fresh-water mussels, says on this point:[11]

"Where formerly really gigantic pond mussels were found, now only quite small ones occur; and it is well known that the European oysters are gradually becoming smaller. This results from the circumstance that both these mollusks are capable of reproduction while they are still quite small, and now never grow to their full size, because they are destroyed before they have accomplished their full growth."

A probable fossil example is the dwarf fauna of the Ohio Black shale.

4. *Variations in Temperature.*—The influence of temperature upon the size of the animal is well illustrated by an experiment of Semper:[12]

"I found by experiment that this animal (*Limnæa stagnalis*) when young first begins to assimilate food, and consequently to grow, when the water is about 12° C.; at the same time a temperature much below has no injurious effects on the animal's life, though it entirely prevents its growth. . . . Assuming that a young Limnæa were placed in a lake or stream of which the temperature constantly exceeds the minimum at which the snail can begin to grow, during only two months of the year, while it never perhaps reaches the high optimum 25°, the mollusk will be unable to attain its due proportions during the first year, or to grow to its full size even during the second, and thus a dwarfed form will inevitably arise. This dwarfed form will still be able to reproduce and multiply itself, for the maturation of germinal matter—the ovum and the sperm—takes place during the winter and early spring, at a time when the low temperature of the water hinders all growth. The optimum of warmth for sexual processes is much lower than that for growth. Thus a permanently diminutive race might arise if the conditions of temperature above described remained constant for several succeeding years in the lake or streams in which the young mollusks or the eggs have been deposited."

But not only does too low a temperature produce dwarfing but when the temperate or polar species are introduced into water warmer than their optimum, they likewise become smaller.[13]

[11] Semper. Animal Life as affected by the Natural Conditions of Existence. D. Appleton and Co., 1881, p. 425.

[12] *Loc. cit.*, pp. 108 and 109.

[13] Semper. *Loc. cit.*, p. 118.

Dall says:[14] "As in mammals and birds so in Pectens the same species in the northern part of its range is larger than in the south unless its habitat is distinctly tropical."[15] So too the slight excess of temperature, 3° within the Mediterranean over that of the Atlantic in corresponding latitudes may help to cause the dwarf fauna within that basin.

Möbius mentions[16] that the same mollusks living on the coast of Greenland and in the Baltic Sea are in the former very large and in the latter small and thin-shelled; this variation he attributes to the constant temperature in the former case and the very great extremes in the latter.

The dwarf faunas of the Black and Caspian Seas are doubtless partly due, according to Forbes,[17] to the great extremes in temperature which they experience between winter and summer.

5. *Change due to Extremes in Depth of Water.*—For each organism there are certain limits of depth of water in which it best flourishes; outside of these in either direction there naturally results a tendency towards pauperization.

(*a*) *Very Shallow Pools.*—Semper[18] took specimens of *Limnæa stagnalis,* hatched from the same mass of eggs, and placed them in aquaria containing different volumes of water. "All the animals were under equally favorable conditions" (as to food, temperature, gases, etc.) "irrespective only of the volume of water which fell to each animal's share; this varied at most between 100 and 2,000 c.c." The result showed that "the smaller the volume of water which fell to the share of each animal, the shorter the shell remained." The number of whorls was the same, four, but the average length of the shell in the 100 c.c. of water was $\frac{1}{4}$-inch, while in the 2,000 c.c. volume it was $\frac{3}{4}$-inch.

[14] Arnold. U. S. G. S. Professional Paper 47, p. 133.

[15] See also Weller, Pal. N. J., 4, p. 77.

[16] Semper. *Loc. cit.*, p. 132.

[17] *Loc. cit.*, p. 211.

[18] *Loc. cit.*, p. 161.

(These measurements were taken from the figures.)

(*b*) *Great Depths.*—The pauperization of faunas with increase in depth appears to be due primarily to the decrease in light, which is essential to plant growth, and thus indirectly to animal life. Secondarily it is due to the decrease in temperature, the increase in the heavier contents of the water, and the greater pressure with depth.

In Geneva Lake the deep fauna is small and sluggish while their surface representatives are larger and active.

In abyssal ocean faunas there are few mollusca, and these are small, translucent, and white, with few crabs and annelids, but many echinoderms and porifera.[19]

With decrease in size from higher to deeper regions there is further pauperization, evidenced in the loss of brilliant coloring and variety of pattern. In the Mediterranean the proportion of colored to uncolored shells at depths of 35 to 55 fathoms is 1 to 3; at 100 fathoms and over, it is 1 to 18.[20]

The very many dwarf or depauperate fossil faunas already noted in the literature are doubtless but a small fraction of those still unnoted. The causes which are active at present in effecting this result were very probably equally active during each year of each era somewhere upon the earth's surface; so that the total number of such examples must be very great. Some of the fossil faunas, as for example, that of the Genesee, consist of uniformly small species, a selective agency having discarded the larger ones; here no stunting of growth is apparent. In such other faunas as that of the Pyrite bed of the Tully horizon, all of the individuals are smaller than the normal individuals of those species, thus showing very decidedly the stunting effect of environment. In still other cases, such as the Tertiary deposits at Steinheim, only a portion of the species were affected unfavorably by the environment, becoming dwarfed in size or of a bizarre shape, while the rest of the fauna were of the normal size for the species.

[19] Heilprin. Geographical Distribution, p. 262.

[20] Forbes. *Loc. cit.*, p. 189.

The following few dwarf faunas are described in illustration of the preceding agencies:

a. Faunas of the Cobleskill, Rondout, Manlius and Bertie of New York.

b. Faunas of the Pyrite bed of the Tully horizon and of the Clinton iron ore.

c. Fauna of the Genesee and Ohio shales; Styliolina limestone of New York.

d. Fauna of the Windsor (Nova Scotia) Carboniferous.

e. Faunas of the Permian.

f. Upper Cretaceous fauna of New Mexico and southern Colorado.

g. Tertiary lake fauna of Steinheim, Germany.

h. Pleistocene ? fauna of the lower Hudson River.

a. The Manlius, Rondout and Cobleskill formations of eastern New York, as well as the Bertie of the western part of the state are conspicuous for their dwarf faunas. The cause was probably in part the greater density of the water and in part the presence of lime mud, making the waters impure mechanically. The section of the rocks at Howes Cave is as follows:[21]

Coeymans, a typical lime sand rock (calcarenite).

Manlius, a fully laminated lime mud rock (calcilutite) with occasional beds of a lime sand.

Rondout, lithology as in Manlius but more argillaceous in upper portion.

Cobleskill (Coralline), lithology about the same as Manlius.

(Slight disconformity.)

Brayman (upper Salina), possibly the equivalent of the Bertie of western New York. Shales gray to green with traces of gypsum. Many iron nodules.[22]

(Great disconformity.)

Lorraine.

Deposition was probably continuous from the Cobleskill to the Coeymans, as there is no evidence of a stratigraphic

[21] Hartnagel. N. Y. State Mus. Bull. 69, p. 1114.

[22] Grabau. N. Y. State Mus. Bull. 69, p. 101.

break. That some at least of these beds were deposited in shallow water and even exposed at times to the sun is shown by the presence of cross bedding, ripple marks, and mud cracks. As is usually the case, these faunas show more strongly their dwarfed condition when viewed as a whole than when distinct individuals are considered; for the reduction in size has not been very great in individual cases, but is shown slightly in nearly all of the forms. For example, *Whitfieldella nucleolata* is equally small in all three of the formations (Cobleskill, Rondout and Manlius); the Spirifers, likewise, are conspicuous for their small size, *S. corallinensis* and *S. eriensis* from the two lower horizons and *S. vanuxemi* from the Manlius. *Favosites precedens* is a small form of *F. helderbergiæ* found in the two lower horizons. The presence of a lime mud seems to indicate that the waters in which deposition took place was denser with alkalies than normal sea water, otherwise the mud would have gone into solution as is usually the case when limestone is eroded. Such abnormal conditions would have a dwarfing effect upon the individuals living there, as has been noted in the case of the Mediterranean. To this unfavorable influence would be added the mechanical impurities of the mud, for on account of the shallowness of the water, the mud would probably be kept by the waves in an almost constant state of suspension. The occurrence of these dwarf faunas between the periods of small exceedingly dense seas or lakes, depositing salt and gypsum, and the normal marine conditions of the Helderbergian is an additional proof of the greater-than-normal density of the water at that time.

b. An exceedingly interesting dwarf fauna is that of the Pyrite layer in western New York at the horizon of the Tully limestone, but where that stratum is otherwise missing. This fauna is very fully discussed by Professor F. B. Loomis.[23]

The layer is a more or less discontinuous deposit of pyrite, appearing as very broad lenses but not over 1 foot in thickness. It contains a fauna of not less than 45

[23] N. Y. State Mus. Bull. 69, 892–920.

species, few of which, though adults, are over 2 mm. in diameter. The fauna includes 1 blastoid, 15 brachiopods, 12 pelecypods, 6 gastropods, 2 pteropods, 7 cephalopods, 1 trilobite, and 2 ostracods. These have all, however, been dwarfed until their average size is only one fifteenth that of the same species in the preceding Hamilton. The cause of this dwarfing is suggested to be the presence of much iron in solution and the gases arising from the decaying vegetable and animal matter. "The iron in the water, as ferrous carbonate, was probably precipitated by the sulfuretted hydrogen" from the organic matter, and thus formed pyrite ($FeOCO_2 + H_2S = FeS + CO_2 + H_2O$).[24]

That iron in the water has a dwarfing effect was shown by experiments upon fishes and tadpoles[25] which in eight months had been retarded in growth from three to five mm. The same is apparently shown in the fauna of the oolitic iron ore of the Clinton beds; in these beds at Rochester, N. Y., the species have "an average of about one third the diameter of the same species in the beds just above and below."[26]

The same condition was noticed in similar beds in Kentucky.

The following list will give a general view of the average size of the dwarfed forms. Loomis gives the average measurement of each species.

Spirifer fimbriatus mut. *pygmæus* Loomis is shown to be one twenty-fifth the normal size of the species.

Nucleospira concinna mut. *pygmæa* Loomis is one fifteenth that of the species.

Tropidoleptus carinatus mut. *pygmæus* Loomis is one fifteenth.

Nucula lirata mut. *pygmæa* Loomis averages one tenth the size of the normal species.

Paracyclas lirata mut. *pygmæa* Loomis is only one twentieth.

[24] *Loc. cit.*, p. 920.

[25] *Loc. cit.*, p. 895.

[26] *Loc. cit.*, p. 895.

The same species of gastropods and cephalopods vary considerably in size, much more so than do the brachiopods.

Since "iron solution in water tends to settle gradually to the bottom, as was found in experimenting on the fishes . . . it is not surprising to find that the brachiopods, which are either sessile or lie on the bottom, are the most dwarfed."[27] The brachiopods are seldom one fifteenth the normal in size, nor do they vary much from this; while the gastropods and cephalopods, groups of greater freedom of motion often vary in the same species from one twenty-fifth to one half the normal size; those which evidently grew up in this iron water being much smaller than those which entered it when partly grown. "All of these fossils then represent cases of arrested development, with the understanding that the arrest is at no given point but all through the development."[28] It is thus a case rather of retarded development or bradygenesis.

These retarded individuals appear like the young of earlier Devonian types.

c. From analogy with the Black Sea deposit, Clarke[29] conceives that the black, very thinly and evenly laminated shales of the Genesee in western New York, with their dwarf invertebrate fauna and fish, with their abundant segregation of iron sulfide, limestone nodules, etc., are likewise the result of accumulation in waters of great depth and imperfect vertical circulation. Dr. Clarke notes the presence of surface ocean currents in this region. He thus interprets the Styliolina limestone, four to six inches thick, at the base of the Genesee in western New York, as essentially a pteropod ooze caused by the meeting of a cold northern current and a warm southern one bearing these pteropods. The cold current thus acted as a barrier to the northwest spread of these pteropods.

An accessory agent in the production of this dwarf

[27] *Loc. cit.*, 898.
[28] *Loc. cit.*, p. 900.
[29] *Loc. cit.*, p. 201.

fauna of the Genesee may have been the presence of a sargasso sea as suggested years ago by Newberry for a similar fauna in the Ohio black shales.[30] The Genesee and Ohio black shales, occurring from New York to Virginia and west to Kentucky and Indiana, contain throughout their whole extent some or all of the following small species: *Lingula spatulata, L. ligea, Schizobolus concentricus, Chonetes scitulus, Leiorhynchus quadricostatus.* These species are not only small, but also thin, the largest or last named being very frequently if not usually crushed through the pressure of the overlying sediment. This smallness and thinness apparently indicates a habitat for the living animals where they were not subjected to the shock of waves as are shore-living species.

d. At Windsor, Nova Scotia, a very fossiliferous limestone, of Carboniferous age, occurs between conglomerate, sandstone and a black shale of the same age below and coal measures of sandstone and coal above. The coal is seen in the Joggins region across the bay. The shallow water or terrestrial origin of the former set of beds is indicated by the predominance of the coarse clastic sediment, the presence of ripple marks, footprints and Lepidodendra. A similar origin accounts for the latter.

The fossils of these Carboniferous limestones show the effect of the unfavorable environment in which they lived at the time these limstones were being deposited. Brachiopods suffer most, being depauperate throughout the series, the pelecypods, though much dwarfed, suffer less diminution, while the cephalopods were the most resistant to the dwarfing agencies; *i. e.*, the more closely a species was confined to a particular habitat the more dwarfed were the resultant adult forms.

The uniformly small size of most of the species is attributed by Dawson to two causes:[31]

1. Variation in depth and content of the water as

[30] Williams. U. S. G. S. Bull. 210, 110.

[31] Acad. Geol., p. 284.

illustrated by one layer which is brown and impure, indicating deposition in shallow and turbid water. In this layer the brachiopods are especially small and depauperate. *Productus cora* rarely reaches one inch in diameter and the Rhynchonellas are minute. The pelecypods are very abundant but dwarfed.

2. The influence of the formation of the beds of gypsum and gypseous marls at the time these limestone reefs were growing. Dawson ascribes the formation of these gypsum deposits to chemical change produced on the calcareous beds and reefs by contact of streams charged with H_2SO_4. Such streams are easily accounted for by the volcanic activity known to have occurred in this region while the shell beds were growing. The great amount of CO_2 released in the change from calcareous carbonate to gypsum would surely render unfavorable the water in which these limestone-secreting animals were living.

e. De Lapparent attributes the depauperized fauna of the Mediterranean in part to the greater preponderance of CO_2 in the water of that sea over that of the Atlantic.

One of the most notable facts arising from a study of red strata is the very frequent total absence in them of all fossils and the often dwarfed and impoverished faunas of the associated strata of other colors. Such red beds are especially conspicuous in the rocks of the Devonian, Permian and Triassic eras. Geikie mentions that fossils are practically absent from the red strata of the Old Red sandstone of England, but abound in the gray or black.[32]

According to the same author[33] "the impoverished fauna of the Permian rocks of central Europe is found almost wholly in the limestone and brown shales, the red conglomerate and sandstone being, as a rule, devoid of organic contents."

In speaking of these same rocks de Lapparent[34] says that "in northern Europe the mollusks of the upper

[32] Textbook of Geol., 2, 1002.
[33] *Loc. cit.*, p. 1066.
[34] Traite de Geologie, 5th ed., 1, 1017.

Permian are always of small size as if they had lived in particularly unfavorable conditions.'' The cause he gives is that ''there was formed a series of interior seas, soon dried up and where the excess of saltness had the effect of injuring the development of the mollusks. These seas have left here and there important deposits of salt and gypsum.''

That this dwarfed fauna was not the normal, open-sea fauna of the Permian is noted by a comparison with the species of the Alps, the Mediterranean region, and India. While in northern Europe the predominating forms are pelecypods and brachiopods, with exceedingly few cephalopods, in these latter more normal regions, the cephalopods become very numerous and all are of a larger size.[35]

It is interesting to note the resemblance of the fauna of the Carboniferous of Windsor, Nova Scotia, to that of the Permian of northern Europe. According to the determination of de Verneuil[36] several species of brachiopods and pelecypods are common to the two regions, showing that similar conditions tend to bring about development along similar lines.

(In this connection Schuchert's discussion of the question—Is there a Permian system or only a Permian formation?—is enlightening.)[37]

f. The dwarf fauna of the Cretaceous strata of New Mexico and southern Colorado[38] occurs in sandy shales and shaly sandstones, accompanied by innumerable fragments of wood. Cross bedding is frequent. The majority of the shells are of normal size, but with these occur many others which are distinctly smaller than in other regions. *Lima utahensis* Stanton is here only one half as large and *Lucina subundata* M. and H. is also smaller than in Utah. *Ostrea anomioides* var. *nanus* Johnson is

[35] De Lapparent. *Loc. cit.*, p. 1067.

[36] Davidson. *Jour. of Geol. Soc.*, 1863, p. 160.

[37] *A. J. S.*, 22, 29–46 and 143–158, 1906.

[38] Stanton. U. S. G. S. Bull. 106. Shimer and Blodgett. *A. J. S.*, 25, 67.

a dwarf form of the species *O. anomioides* Meek. *Ostrea lugubris* Conrad is a small species resembling the large *O. blackii.*

A probable explanation of this fauna and its habitat may be drawn from Metzger's observations[39] upon that much-studied shell, *Cardium edule.* This upon the sand shoals of the ocean flats is small, while it attains its maximum size off the rugged coasts of Norway and Scotland. These Cretaceous strata with their sand, cross-bedding, much fragmentary wood, and a marine fauna indicate a shallow sea into which emptied some large river, a condition probably somewhat similar to that of the eastern part of the North Sea at present.

g. It often happens that while a portion of a certain fauna is dwarfed, the rest are of normal size. Hyatt[40] discusses an excellent example of this mixture of dwarf and normal forms from the Tertiary strata of Steinheim, northwestern Germany.

Into the Tertiary lake at Steinheim migrated four varieties of *Planorbis levis.* The descendants of these are divided into the progressive series or those which became larger and more robust, and the retrogressive or those which became smaller, less robust and distorted.

The dwarfing of the one series may be explained as a sapping of the individual's energy due to its being in an unfavorable environment. It is common to note signs of old age appearing immediately after a severe injury to the animal.[42]

In gastropods this is often indicated by uncoiling and rounding of the whorls, so that these may be looked upon as signs of weakness in the animal. Hyatt discusses the reason for this as follows:

"Among living animals it is a matter of daily experience to find some races incapable of enduring variation in the surroundings to which others readily accommodate themselves and even thrive under."[41]

[39] Walther. Einl. in die Geol., p. 32.

[40] The Genesis of the Tertiary Species of Planorbis at Steinheim. *Bos. Soc. Nat. Hist. Anniv. Mem.,* 1880.

[41] Hyatt. *Loc. cit.,* p. 16.

[42] Shimer. Old Age in Brachiopoda. AM. NAT., 40, 115.

"In the individual the effects are shown in the disturbance of the laws of growth, producing abnormal or premature weakness or in the natural exhaustion of the powers of growth causing senility. A wound and its results, whatever they may be, can unquestionably be so classified, since it is primarily a severe shock to the system which lays additional burdens upon the powers of growth and is usually followed if severe by retrogressive metamorphoses or premature old age . . . normal old age simply expresses the normal wearing out of the powers of vitalized tissue to sustain itself against the perpetual friction of existing physical surroundings. . . . When we compare these effects of unfavorable environment in producing distortion and decrease in size of the individual with the corresponding distortions and decrease in size of the retrogressive sub-series there is a certain similarity which leads to the supposition that the latter are also probably due to an unfavorable environment." [43]

h. At Storm King, about fifty miles above New York, was found in drilling a series of holes across the Hudson, an apparently dwarf fauna including only two species, *Mulinia lateralis* (Say), of which there are hundreds of specimens and *Trivia trivittata* Say, of which there are but few specimens in our collection.

(These fossils were obtained by Professor W. O. Crosby in February, 1908, and through his kindness these facts are presented.)

These were found in but one drill hole, though probably the same species are present in the others but passed unnoticed in the drilling. They occur 620 feet out in the river from the Storm King shore, 40 feet below the bed of the river, *i. e.*, about 120 feet below the present river or sea level at that point. The Hudson is brackish at this point and as far north as Poughkeepsie, as is evidenced by the absence of ice houses below Poughkeepsie. Whether in the present bed of the stream there are any marine forms growing was not ascertained. The heavier sea water might still come up in sufficient amount to furnish a marine habitat even under quite fresh surface conditions. This dwarf fauna in the abundance of *Mulinia lateralis* suggests Pleistocene age.

These two species live at present off the New England

[43] Hyatt. *Loc. cit.*, p. 15.

and New Jersey coasts, in normal marine or but slightly freshened water. An average-sized fossil specimen of *Trivia trivittata* is three eighth inch long with a greatest diameter of three sixteenth inch. An average size for those off the Massachusetts coast is two third inch by one third inch. The smaller specimen is less strongly ribbed and less nodose.

One of the larger of the fossil specimens of *Mulinia lateralis* measures five sixteenth inch by one fourth inch. The young shells off the coast are small, thin, with margins subequally rounded and beaks inconspicuous and nearly touching each other; this description applies to all of the Hudson River specimens. It does not seem probable, however, though possible, that so many shells could be gathered at random as was done by the drill without getting some adults. The more probable explanation seems to be that these fossil individuals were living in an unfavorable environment, a water less than normally saline, and through a consequent sapping of vitality, were not able to attain large size.

Summary

In the first part of the above discussion was given what appear to be some of the principal causes for the dwarfing of invertebrate water-living faunas; these were illustrated by present-day examples. In the second part a few fossil examples are described with a brief discussion of the probable cause of the dwarfing in each case.

The chief agency is apparently an abnormal habitat. A species, for generations used to an environment of sea water with a certain unvarying density, temperature, clearness and depth, would become so accustomed to that state of affairs that a change in one or more of the factors would affect it unfavorably. An unfavorable environment causes a greater expenditure of vitality in the continuance of life than does a favorable one. Hence after the maintenance of life itself, there would be less surplus energy left for growth. There would thus result a

tendency to smallness of size especially in those species having comparatively little vitality to start with. It could happen then that from this cause alone either all or but a few of the species of a fauna would become dwarfed.

The hard parts of the animal are so intimately related to the soft parts that whatever affects the soft parts is immediately impressed upon the building shell. Thus whatever ill or good conditions the animal is subjected to are expressed in the shell, as are moist and dry summers recorded by the annual rings of exogenous trees.

Two classes of dwarf faunas are noted: (1) Faunas where the individuals are of smaller size than that to which the species grows under normal conditions; this is the resultant of an abnormal habitat. (2) Faunas where all the individuals are small but of the normal size of the species; in this case some selective action has weeded out all the large and heavy species, leaving a dwarf but not stunted fauna. Dwarf faunas usually include representatives of both these classes.

Dwarfing shows itself in two ways:

1. An acquirement of old age characters by the dwarfed animal. Such old age characters as sluggishness, loss of external sculpture, teeth, etc., are very common in stunted forms.

2. A retention of youthful characters. That is, the animal's growth takes place so slowly, due to the abnormal environment that saps the vitality, that death overtakes it before it has passed through the youthful stage, and the animal develops no old age characters.

NOTES AND LITERATURE

ICHTHYOLOGY

Life History of the Eel.[1]—The waters of the northeastern Atlantic and of the adjacent North and Baltic Seas have been subjected in recent years to a most elaborate and continuous investigation, thanks to government subsidies and international cooperation. A coordinated study of the plankton and an investigation of the breeding habits and the young of the important food fishes and of their migrations and movements, have made up the large part of the ambitious program of this International Commission. In the allotment of the field it has fallen to the Danish Fisheries Bureau to undertake to complete our knowledge of the life-history of the common eel. Dr. Johs. Schmidt, with the aid of the Danish fisheries steamer *Thor* and Dr. Petersen's young-fish trawl, has added a new, and almost final, chapter in the solution of this mystery which has puzzled naturalists for centuries.

The suggestion of Dr. Theo. Gill in 1864 that the peculiar ribbon-like fish known as Leptocephalus was the larva of the Conger eel was subsequently verified by Dareste's (1874) anatomical comparisons and Delage's (1886) successful rearing of a Leptocephalus through its metamorphosis into the Conger eel. It remained for the Italian zoologists Grassi and Calandruccio to demonstrate in 1897 that the larva known as *Leptocephalus brevirostris* was in reality the young of the common European eel, *Anguilla vulgaris.* Their conclusions were based upon anatomical comparisons, transitional stages, and experimental rearing of the larval Leptocephalus to the young Anguilla. Most, if not all, of the material upon which the work of the Italian investigations were based was obtained at or near the Straits of Messina where the famous whirlpools bring to the surface the organisms of the deeper waters.

The eel fisheries of northern Europe are widespread and in places, especially in the Baltic Sea, they are extensive. There were in 1881, 18,491 eel traps in operation along the Swedish

[1] Contributions to the Life-History of the Eel (*Anguilla vulgaris* Turt.). By Johs. Schmidt. Conseil Perm. Intérnational pour Expl. de la Mer. Rapports et Proces-verbaux, Vol. 5, pp. 137–274, Pls. 7–13.

coast, and in 1900, 22,608 in Danish waters, excluding fresh water and the smaller areas of salt water. Yet in spite of these extensive fisheries and the wide distribution of the eel along the coasts of the Atlantic and its tributary waters in Europe, absolutely nothing has been known of the spawning grounds, or breeding habits of the eels of these more northern waters. Sexually mature eels have rarely, if ever, been taken. Dr. Schmidt records the discovery of but a single sexually mature male eel of the silver (migrating) type in shallow waters off the coast of Denmark. Leptocephalus larvæ belonging to the common eel (*L. brevirostris*) have never been taken, until recently, in the Atlantic. The specimen taken by the Challenger Expedition in the North Atlantic and referred by Günther to this species proves upon reexamination to belong to another species having 140 myomeres instead of the 111–118 characteristic of *L. brevirostris*.

In 1904 a single example of this latter species was captured by Dr. Schmidt in the tow nets of the *Thor* west of the Faeroes, and a few months later Dr. Holt, of the Irish Fisheries Bureau, took a second specimen west of Ireland. These captures gave the clue which Dr. Schmidt has most successfully followed. In the next two years Leptocephalus was discovered by Dr. Schmidt in large numbers in mid-summer to the west of the British Isles and France over depths of 1,000 meters. The transition stages between the hyaline pelagic larvæ in the Leptocephalus stage and the colorless "elvers" which have long been known along the northern and western coasts of Europe were also found by the *Thor* but at the close of summer and in the autumn. After a thoroughgoing investigation of these grounds and of the data regarding the movements and distribution of the young elvers along the coasts of Great Britain and continental Europe Dr. Schmidt comes to the following conclusions.

The common eel of northern Europe spawns in the Atlantic Ocean west of the British Isles and southward at least as far as the northern coast of Spain. The essential features of the spawning ground are (1) a depth of at least 1,000 meters and (2) a temperature at this depth above 7° C. This belt is a relatively narrow one along the edge of the continental shelf as it rises from the Atlantic basin. Leptocephalus larvæ have long been known in the Mediterranean and a much greater extension of the spawning grounds beyond the known limits to the south is not improbable. The Atlantic basin with its greater depths and lower temperatures appears to afford an effectual

barrier between the American and European eels (*Anguilla chryspa* and *A. vulgaris*). Eels of European streams approaching sexual maturity and migrating seaward must travel to the edge of the continental shelf to reach suitable spawning grounds. The Baltic and North Seas are too shallow, and waters to the west of Norway are deep enough but their temperatures are too low.

The eels, as they migrate, undergo a considerable change in appearance, passing from the stage known as the yellow eel to that of the silver eel, in which feeding is suspended, the digestive tract is shrunken and sexual glands show some enlargement. The direction of migration in the Baltic in the autumn is out toward the open sea. The paths of migration are usually parallel to the coast and in shallow water, though eels have been known to cross channels 60 meters in depth. The direction and rate of migration was worked out by Dr. C. G. Joh. Petersen, the director of the Danish Fisheries Laboratory, by means of marked fish. The rate of movement in the migratory season is about 15 kilometers per day. The eels in these shallow waters, where their presence is revealed by commercial fishing, are none of them sexually mature. Their further movements are unknown but the presumption is that they continue their course toward the open sea and to the edge of the continental shelf. A single capture in the English Channel twenty miles from land confirms this conjecture, as do also the captures made by Grassi and Calandruccio in the whirlpools at Messina, where occasional specimens of the common eel are brought to the surface, which differ materially from those taken in shallow waters. They are silver eels in which the breeding dress is further accentuated by darker color, the anterior border of the gill openings and the pectorals become an intense black, the eyes also become enormously enlarged and the sexual organs show greater maturity. Maturing eels have also been taken from the stomachs of the sword-fish and in the collection of Prince Albert of Monaco is a large eel taken from the stomach of the cachelot. These facts in conjunction with certain testimony on the part of fishermen suggest the possibility of a pelagic or bathypelagic habitat of the eel in its migration to the open sea.

The larvæ *Leptocephalus brevirostris* of the eel are true pelagic organisms, as is shown by their entire organization. Neither their structure nor their distribution indicates any relation to a bottom habitat. In life they are perfectly transparent

and are found in association with typically pelagic organisms such as Salpa, Cymbulia and Phronima, as well as the young of other pelagic or deep-sea fish, among which are five additional species of "Leptocephalus." They have also the leisurely movements characteristic of many pelagic animals.

The pre-Leptocephalus stages of the eel are as yet wholly unknown. The earliest season of investigation has been the month of May and at this time the pelagic larvæ are found during the day in greatest abundance in levels at a depth of about 100 m., but rise to the surface levels at night. This distribution of the youngest known stages leads Dr. Schmidt to surmise that the eggs of the common eel are bathypelagic, and that the larvæ as they develop rise to the upper levels.

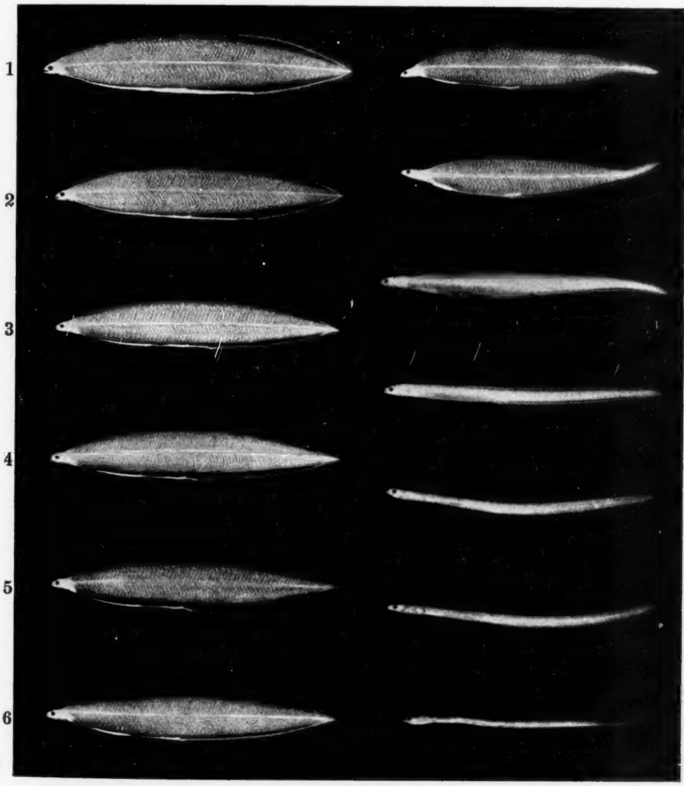
The pelagic larvæ appear to reach the height of the larval stage of development in June and cease active feeding, but do not as yet show the regressive phenomena which characterize the period of metamorphosis. They have also reached their maximum larval size 75 (60–88) mm. Both upper and lower jaws are equipped with long slender grasping teeth. No pigment is found in the body except in silvery iris of the eye. The digestive tract at this time extends through about two thirds of the length of the body.

The larval stage is followed by a long period of metamorphosis during which the form of the body changes from that of a colorless ribbon-like band to the pigmented cylindrical type with differentiated head and tail. The pelagic mode of life is abandoned and the young eels or elvers adopt the bottom habitat in shallow coastal and fresh waters into which they have migrated from the open sea. This period of metamorphosis occupies the entire year or more, during which no food is taken. The body gradually decreases in size as the metamorphosis proceeds, diminishing from an average length of 75 millimeters in the high seas in June to 65 millimeters a year later in coastal waters. The digestive tract shortens during this period from two thirds to one third of the total length of the body. Mandibular and vomerine teeth appear and dermal sense organs develop about the head.

During this long period of metamorphosis the Leptocephalus larvæ migrate slowly from their habitat above the 1,000-meter line shoreward. According to the recent summary of observations published by Professor Gilson, they reach the coasts of Spain and Ireland in October–December, and the western coasts

of France and England and the eastern shores of Scotland in January–February. In March the tiny elvers swarm along the shores of the Netherlands, Denmark and Norway and continue to arrive there during the month of May. Danish waters and the western Baltic form the eastern limits which the eel reaches in the elver stage. Their farther migrations into the Baltic and up the rivers of northern Europe are accomplished during the period of rapid growth which now ensues.

The extensive eel fisheries of Europe thus depend upon the migratory habit of a true Atlantic deep-water fish which seeks



Metamorphosis of the Eel (*Anguilla vulgaris*).
Figs. 1–2, 1st stage (*Leptocephalus brevirostris*). Figs. 3–6, 2d stage. Figs. 7–8, 3d stage. Figs. 9–10, 4th stage. Figs. 11–12, 5th stage. Fig. 13, 6th stage.

fresh-water streams and lakes for its period of growth but returns to the deep sea to spawn. CHARLES A. KOFOID.

The Valves in the Heart of Fishes.—The following note by Dr. H. D. Semor, of the College of Medicine in Syracuse University, New York, on the valves in the heart of fishes should be put on record.

It may be noted that in the so-called ganoid fishes there is more than one row of valves and from these ganoid fishes are derived the herring-like fishes. Some of these, as Dr. Senior has noted, have two rows of valves. Others have but a single one as in ordinary fishes.

"With regard to the question of teleosts having a conus arteriosus provided with more than one row of valves: In addition to Albula[1] which has long been known to have two rows, I have found a conus with two rows of valves (each row having two cusps) in *Tarpon atlanticus*,[2] *Megalops cyprinoides*,[3] and in *Pterothrissus gissu*.[4] I think this list will prove to be complete, as I have examined, with a negative result, Elops,[2] Chirocentrus,[5] Chanos,[3] Dorsosoma,[2] Notopterus,[2] Pomolobus,[5] Alosa,[5] Brevoortia,[5] and Boas has examined Osteoglossum.[6]

"A well-marked or vestigial conus arteriosus with *one* row of valves only, occurs in Elops,[4] Hyodon,[5] Chirocentrus,[3] Chanos,[3] Notopterus,[6] Osteoglossum[6] and Dorosoma.[2] That it also occurs in other allied genera, I have little doubt. When I collect enough specimens, I intend to describe and figure the conus (or vestige) in a sufficient number to indicate its mode of disappearance." DAVID S. JORDAN.

PARASITOLOGY

The Hereditary Transmission of Germ Diseases.—The earlier views which favored hereditary transmission of germ diseases have been subjected for nearly half a century to careful scrutiny at the hands of bacteriologists and are now generally rejected. Experimental evidence has been furnished from many quarters that the supposed cases are due to a contamination of the offspring during transit through the maternal passages at birth, or

[1] Stannius. Bemerkungen über das Verhaltniss der Ganoiden zu den Clupeiden, insbesondere zu Butirinus Rostock, 1846. Boaz. *Morph. Jahrb.*, Bd. 6, p. 527.

[2] Senior. *Biol. Bull.*, Vol. XII, p. 146.

[3] Senior. *Biol. Bull.*, Vol. XII, p. 378.

[4] Senior. *Anatomical Record*, Vol. 1, No. 4, p. 82. (*Am. J. of Anatomy*, Vol. VI, No. 4.)

[5] My own notes, unpublished.

[6] Boaz. *Morph. Jahrb.*, Bd. 6, p. 527.

occasionally to infection *in utero*, although in the majority of cases the cord and placenta form a barrier to the transmission of bacteria. Even when the bacteria gain entrance into the fetus there is no adaptation to the reproductive process.

Until very recently the part played by animal organisms in the transmission of diseases has been regarded as of very minor importance, and for the few known instances the same view rules with reference to conditions of transmission as already noted for bacteria. In the case of malaria, the oldest known protozoal disease, many experiments have been made to determine the occurrence of transmission *in utero*, from mother to offspring, and not only the general facts but also the details have been established.

A long series of able investigators, among them our own W. S. Thayer, have found that the malarial organisms present in the maternal blood do not occur in the blood of fetus and of the newborn. It has been generally agreed that these hæmatozoa can not traverse the placenta from the pregnant mother to the fetus. Moreover Bignami et Sereni demonstrated that the fetus lacks not only the parasites, but also the anemia which often characterizes the mother. The subject has been subjected to most careful reexamination at the hands of two Greek investigators.[1] In every case the maternal blood contained malarial parasites in greater or less abundance. In blood taken from the maternal face of the placenta, parasites were abundant, in that from the opposite or fetal face they were absent or very rare. In blood taken from the umbilical cord and from the liver, kidney and other organs at autopsies, not a single parasite was demonstrated. Thus they confirmed absolutely the view that these haematozoa do not traverse the placenta.

An interesting departure from these conditions is afforded by recent investigations on other disease-producing protozoa. The experiments are not extensive and in some cases contradictory. Thus Massaglia[2] infected pregnant guinea-pigs with trypanosomes. In one case at death the liquor amnii contained trypanosomes, in the other not; but in neither case could any parasites be found in the blood of the fetus. On the other hand, Pricolo[3] found in mice a trypanosome which was capable of traversing

[1] Pezopoulos et Cardamatis, *Centr. Bakt. und Par.*, Orig., 43, 181.
[2] *Gaz. Ospedali ed Clinichi*, 1906, 12.
[3] *Centr. Bakt. und Par.*, Orig., 43, 231.

the placenta and affecting the young *in utero*. It also appeared to multiply rapidly in the fetal circulation.

In cases of congenital syphilis, *Treponema pallidum* has been shown to be present in small numbers in the blood taken from placenta and cord and undoubtedly has the power to pass through the placental tissue from maternal to fetal circulation. While a final decision can not be reached at present, the weight of evidence favors the view that Treponema is an animal rather than a bacterium. In some closely related forms the conditions have been more definitely established. Thus in *Spirochaeta duttoni*, the cause of African relapsing fever, Breinl and Kinghorn,[4] in four rats and one guinea-pig, demonstrated the passage of the spirochete through the placenta into the fetus. The parasites were found in the placenta in approximately the same numbers as in the heart blood of the mother, yet in very meager numbers in fetal blood. There was no tendency to abort, yet a large percentage of young died shortly after birth. The spirochetes from fetal heart blood showed themselves virulent on inoculation.

These and similar cases among animal parasites are not surprising. They differ from the accidental contamination of the young at birth in the case of bacterial diseases only in that the infecting agent is capable of migration through solid tissue and thus passes barriers in the placenta which constitute obstacles to the passage not only of bacteria but also of some other animal organisms, like the plasmodium already noted, which do not penetrate tissues, but pass their entire existence in the blood stream. So far as known there is no adaptation of the parasite to special conditions and the infection of the new generation *in utero* does not differ biologically from the infection of a new organ as the parasites wander through the body of the host. The transmission of the disease to a second generation is a biological incident and bears no especial relation to the reproductive organs or function.

Certain cases are known, however, in which the conditions are radically different. One of the first of these was the demonstration by Koch[5] of the life history of *Babesia* (= *Piroplasma*) *bigeminum*. In this he was able to determine that one form in development was found in the eggs of the tick by which the organisms are transmitted. This stage appears to be the means by which the young larvæ of the second generation of ticks are

[4] Liverpool School Trop. Med., Mem. 21.

[5] *Zeit. f. Hyg.*, 54, 1.

infected. It has long been known that young produced by infected ticks will transmit certain diseases even though they have never come in contact individually with cases of the disease. The demonstration in the ova of such forms as discovered by Koch furnishes evidence of the manner of this transmission. Christophers[6] has followed carefully the formation of these bodies and their penetration into the ova, where they become spherical resting stages. He has also traced these bodies through larva to nymph and thinks that when the latter become adult the parasites have migrated into the salivary glands. It has long been known that Texas fever was conveyed by the progeny of infected ticks, but the demonstration of the infective agents has heretofore eluded observation.

Several authors, among whom Carter[7] may be mentioned, have shown that *Spirochaeta Duttoni* infects the ova of ticks which suck the blood of hosts harboring this parasite, that the organisms multiply in the ova and that by them the new generation of ticks is infected and may transmit the disease produced by the parasite. Other instances of the same type might be added to the list. The process may, however, go one step farther.

Recently reported investigations of several observers show that in the housefly a parasitic flagellate infects the ova and thus the subsequent generation of its host. Since the host is no longer a blood-sucking insect, there is no possibility of a sanguinicolous generation of the parasite in some other host. Probably the hereditary method is the only one by which the parasite is propagated and new generations of flies are infected, although it is possible that encysted forms, discharged in the feces, might be taken up in the food of some other fly. It is interesting to note in this connection some work done in my laboratory by Mr. L. D. Swingle, who has followed out the life-history of a similar flagellate parasitic in the sheep-tick. As is well known, this host is really a degenerate fly, and this parasite has, so far as can be ascertained, no relation to the blood-sucking habit of its host. It infects the ova and in a resting stage awaits there the development of the next generation, but no stages were found indicating any other method of transmission.

These instances just outlined differ radically from those noted at first in which the organisms traverse the placenta and gain entrance to the offspring *in utero*. The latter involve, as already

[6] *Indian Med. Gazette*, December, 1906, 467.

[7] *Ann. Trop. Med. and Par.*, 1, 157.

indicated, no modification or adaptation in the process of reproduction. But in the infection of the ova with a resting stage is involved a selection both of the definite organ and of the cell which becomes infected. Further, the parasite must assume a resting condition adapted to undergo successfully the changes indicated in the development of the adult insect from the eggs and sometime in the latter process must reach the suitable location. In the case of the fly such a location will be the alimentary canal of the insect, while in the tick which is to transmit the disease-producing organisms the suitable location will be rather the salivary glands, as suggested by the observations of Christophers. In any event the interrelations are evidently extremely complicated. The infection of the fetus by tissue-penetrating protozoa is purely incidental; the infection of the ova and through them of the second generation is a complicated biological process, involving essential modification in the life-history of the parasite and important morphological adaptations to new conditions of life.

A Society for the Destruction of Vermin.—Recent demonstrations as to the agency of mosquitoes, flies, bedbugs, rats and other household pests in transmitting serious diseases has taken such active hold on the British mind that there has been organized in London a Society for the Destruction of Vermin. It is incorporated under the Board of Trade regulations as a public association not formed for the object of making profit. The work the society has set itself to do is: (1) Collect information from all sources on the distribution and life-history of vermin. It will pay special attention to the part played by vermin in disease causation. (2) Disseminate as widely as possible the acquired knowledge by means of the general press, and also by special reports, leaflets and lectures. It will endeavor to make known to the public the dangers connected with each kind of vermin, the necessity for exterminating certain species, and the best means of destruction. (3) Carry out experiments in the field, test any promising measures suggested for the destruction of vermin, and, if funds permit, distribute gratuitously, to such persons as are unable to afford the expense, the necessary substances and apparatus. (4) Organize, in cooperation with other associations and public bodies, a practical campaign for the destruction of vermin. To conduct operations an active committee has been formed. (5) Encourage and assist in any legitimate

way the operations of rat and sparrow clubs and similar bodies.

The services of the society will be placed at the disposal of municipalities, boards of health, agricultural societies, shipping and deck companies, and other bodies interested in the suppression of vermin. The society has already received the support of many eminent physicians, bacteriologists and chemists, together with that of agricultural and poultry organizations, public associations and other bodies.

H. B. W.

PLANT CYTOLOGY

Polar Organization of Plant Cells.—Research in plant cytology has resulted in conflicting views as to the extent of such polar organization of plant cells as is well known for certain animals from the work of Rabl, Van Beneden, Flemming and others. Some of the algæ present clear evidence of such polarity, the best known example being Stypocaulon, which has a center in the form of an aster with a centrosome, present at the side of the resting nucleus and dividing previous to each nuclear division, or mitosis, to establish the poles of the spindle. A similar aster is present at the tetraspore mother-cells of Dictyota. Other algæ such as Fucus and Corallina show highly developed centrospheres at the poles of the spindles, but investigations so far indicate that they are formed *de novo* with each mitosis and that there are no permanent centers associated with the resting nuclei to give polarity to the cells.

The research of recent years on the cells (particularly the spore mother-cells) of pteridophytes and spermatophytes has failed to support certain claims for the presence of centrosomes in these groups of plants, and has indicated that their cells are without visible polar organization. As nuclear division approaches in the spore mother-cell fibrillæ appear in the cytoplasm, at first arranged radially, but later becoming associated in cone-shaped groups (constituting the multipolar stage), and at last arranging themselves to form the two opposite poles of the final bipolar spindle. Among the bryophytes, the liverworts have received considerable attention. In this group well-differentiated centrospheres are present at the poles of the spindles, but these are described by all investigators as arising *de novo* and they have not been reported in association with the resting nuclei.

The subject of polar organization in plant cells has received especial attention recently through the work of Harper[1] on the mildews (particularly Phyllactinia), and that of his student Marquette[2] on Isoetes and Marsilia. Harper found in the ascus of Phyllactinia an especially favorable subject for the study of the organization of the resting nucleus and its mitosis in relation to a central body, which is a permanent organ of the cell and gives to the nucleus and cell a definite polar organization. The central body lies on the nuclear membrane and the chromatin elements in an early stage of mitosis have the form of strands, each one attached independently to this center. Even in the resting nucleus, when the chromatin has the structure of a network, its attachment to the central body is evident and indicates that the strands have an individual connection with the central body as a nuclear pole. During the prophase of mitosis the central body divides and the two portions move apart to become the poles of spindle and, at the completion of mitosis, each remains connected with a daughter nucleus, thus maintaining its polarity. Furthermore, in the process of nuclear fusion within the ascus each nucleus contributes its complete polar organization so that the resulting fusion nucleus has for a time two central bodies and two independent groups of chromatic elements, which later gradually fuse into a single system with one central body.

Marquette has discovered a remarkable polarity in the leaf cells of Isoetes. Each resting cell contains a large starch-containing body, which lies so closely pressed against the side of the nucleus that the latter is usually indented. Sometimes the body is present without the starch grains that usually render it very conspicuous. Previous to nuclear division this polar structure elongates and divides by constriction and the two parts draw apart so as to form a furrow on the surface of the nucleus. The separated halves then come to lie at opposite ends of the nucleus, which has become somewhat elongated. These developments take place before the appearance of the chromatin gives

[1] Harper, R. A. Sexual Reproduction and the Organization of the Nucleus in Certain Mildews. *Pub. Car. Inst.*, No. 37, 1905.

[2] Marquette, W. Manifestations of Polarity in Plant Cells which Apparently are without Centrosomes. *Beih. Bot. Centralbl.*, XXI, p. 281, 1907. Concerning the Organization of the Spore Mother-cells of *Marsilia quadrifolia*. *Trans. Wis. Acad. Sci. Art. Let.*, XVI, p. 81, 1908.

indication of the approaching mitosis. As the prophases of mitosis become evident the two polar structures move away from the nuclear membrane, become much flattened, and spindle fibers develop in the region between the two. The polar structures then round up so that in the metaphase of mitosis they are irregularly rounded bodies at the poles of the spindle against which the ends of the spindle fibers press. During anaphase the chromatin of the daughter nuclei comes to lie closely against the surface of the rounded polar structures, and each daughter nucleus when fully formed is deeply indented or kidney-shaped in sections. The amount of starch decreases during the prophases, indicating that there is a consumption of starch at the time of the mitosis. The polar structures increase in size during telophase and remain at the side of the daughter nuclei until the above history is repeated with the next mitosis.

In the spore mother-cells of Marsilia, Marquette has found evidence of polar organization at the time of synapsis. Following the differentiation of the spore mother-cells there is a period of growth during which starch grains appear, first in a scattered arrangement, but soon in a specified region between the nucleus and the wall of the spore case, a situation favorable for an interchange of metabolic movements between the nucleus and the surrounding tapetum. There is thus a polarity of the cell, which presently becomes more conspicuous by the changes characteristic of synapsis within the nucleus. The chromatic material during synapsis converges to a point on the nuclear membrane against which lies a nucleole, and the entire mass of contracted chromatin is directly opposite the assemblage of starch grains in the cytoplasm adjacent to the nucleus. The nucleus, then, during synapsis presents a definite polar side with its chromatin content contracted at a point opposite the assemblage of starch grains, and an antipolar side free from chromatic substance, where also the nuclear membrane appears much heavier than in the region of the synaptic mass.

Fibers become conspicuous in the cytoplasm during synapsis, especially on the antipolar side of the nucleus, and these tend to become arranged in cone-shaped groups as the nucleus passes out of synapsis. There is at times a bipolar arrangement of the fibers, but later several well-defined poles are developed and a multipolar stage results which is similar to the multipolar spindle characteristic of spore mother-cells. The cones of the